PATTERNS OF RECRUITMENT, GROWTH AND MORTALITY OF THE MUSSEL, MYTILUS GALLOPROVINCIALIS IN RELATION TO WAVE EXPOSURE AND TIDAL ELEVATION.

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ABSTRACT

Population patterns of the alien mussel *Mytilus galloprovincialis* were investigated at two locations on the west coast of South Africa: Camps Bay and Groenrivier. Specifically, wave exposure and zonation were examined for their effect on mussel cover and total density, mussel size and recruit intensity. Two areas were compared at Camps Bay; the first was a prominent rock experiencing heavy wave action, and the second was a sheltered bay. Three areas were selected at Groenrivier, the third experiencing an intermediate gradient of wave action. A number of interesting patterns emerged, although not all were statistically significant. At both Camps Bay and Groenrivier mussel cover increased with increasing wave exposure and decreased with increasing tidal height. The exception to this zonational trend was exhibited in the very sheltered bay at Groenrivier, where mussel cover increased upshore, from 2% to 6%. Total mussel density and recruit intensity declined with a reduction in wave action at both locations. An unexpected zonational pattern occurred at both Camps Bay and Groenrivier - total densities tended to be greater upshore, a pattern which closely followed recruit densities. The maximum size achieved by mussels is greatest at more exposed areas, but the difference between sheltered and exposed regions at Camps Bay was not notable. Maximum shell size tended to decrease with increasing tidal height in all areas but the sheltered bay at Groenrivier, where little variation in maximum size occurred. Multivariate comparisons of population demography between all of the sites revealed that the sheltered site at Camps Bay was most similar to the semi-exposed site at Groenrivier, which points to similar environmental conditions in these areas. This pattern was repeated for total densities, a result which supports the previous suggestion. The sheltered bay at Groenrivier was most dissimilar in both demographic structure and density to all other sites.

The previous analyses suggested that recruitment strongly influenced some of the population patterns identified and this was explored further at the Camps Bay study site. Data were collected monthly, from June to September 1993, when recruitment is greatest. The trends in recruitment intensity, described above, persisted in this analysis and showed no temporal variation over the experimental period. Recruitment to artificial collectors suggested that increased mortality in the low shores of both exposed and sheltered areas is responsible for the higher natural recruit densities recorded upshore. Similar patterns of mortality were evident from examination of young mussels, using the method of cohort analysis. Adult densities, like recruit densities were highest in the wave exposed region and increased upshore. There was a great deal of spatial variation in the recruit-adult density relationship, and this relationship varied from month to month and was generally poor. Monthly data pooled for each site revealed that a very small proportion of adult density (3%) is explained by recruit density at the exposed low and high-shore sites as well as at the sheltered low site.

The relationship was significant at the sheltered high-shore site, where 27% of the variation in adult density was accounted for by recruitment. The relationship between adult density and recruit density for the whole of the Camps Bay study area over the four month period was significant, but only 19% of variability in adult densities was accounted for. Comparisons of size-frequency composition, using multidimensional scaling and hierarchical cluster analysis, indicated that the sheltered low site is most similar to the exposed low site an the two high-shore sites are most similar to each other, a result which presumably reflects environmental similarities. A notable outcome of the analyses was that this pattern showed no temporal variation.

Growth and mortality was compared at different grades of wave action and at different tidal heights at Camps Bay to determine their effects on the population patterns described previously. Examination of the relative growth rates of "tagged" adults agreed with results obtained by cohort analysis, performed on the full size range of mussels. Mussels grew faster at the exposed area than at the sheltered bay, which accounts for the greater size achieved by mussels at the former location. Similarly, growth rates determined separately for the low shore sites and the high shore sites provide an explanation for the trends in mussel size recorded previously: growth rates were lower at higher tidal levels and mussels attained relatively small maximum sizes here. More specifically, growth rates were highest at the exposed low site, followed by the sheltered low site and the exposed high site. Mussels at the sheltered high site grew relatively slowly. A separate collection of newly recruited mussels from low-shore zones in the exposed and sheltered areas indicated that these mussels had comparable growth rates as well as mortality rates over a two month period. These results are not in agreement with results obtained from the cohort analysis technique (by separation of the first cohort). It remains to be seen whether differences in growth and mortality emerge over longer periods. Mortality of labelled adults was extremely high in the exposed low zone, following severe winter storms. Fewer adults died in both the sheltered low zone and the exposed high zone, and survival was highest at the sheltered high zone.

Spatial variation in disturbance was recorded at Camps Bay during the winter of 1993. Storm-induced wave action removed a $1.4m^2$ of mussel bed from the exposed low shore, compared with less than $0.27m^2$ from each of the remaining four sites. Areas disturbed were immediately adjacent to previously cleared experimental plots. Measurements of strength of attachment and shell length were taken at each site to determine whether a) the differences in area disturbed was related to the force required to dislodge mussels, b) any "edge" effects occurred and c) temporal variation occurred. Within-bed mussels in the low zones of exposed and sheltered zones were more firmly attached than those in the higher zones and differences were at least partly related to their greater size. Mussels situated on the edges of plots were

relatively weakly attached compared with within-bed mussels, at the exposed low and high shore sites and at the sheltered low site. This "edge" effect was not evident two weeks later at the two former sites because "edge" mussels were more firmly attached. This is most interesting considering that mussels within the bed were also more firmly attached at this time. No "edge" effect or "temporal" effect was recorded at the sheltered high-shore site.

These findings illustrate some of the processes that influence population patterns *of M. galloprovincialis* in relation to wave exposure and vertical position on the shore and the temporal variability that often occurs.

DECLARATION

This dissertation is my own unaided work and is being submitted for the degree of Master of Science in the Zoology Department, University of Cape Town. It has not been previously submitted in whole or in part for any degree or examination in any other university.

Signed by candidate

29/3/95

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GENERAL INTRODUCTION

There is an increasing awareness in marine ecology that the patterns we observe and the mechanisms that cause them are scale-dependent (see e.g. Wethey, 1984, Menge, 1991). Community structure is influenced by a hierarchy of processes (see e.g. Allen and Starr, 1982), from fine-scale biological interactions such as predation and competition to the broader-scale effects of larval supply and oceanographic currents. Disturbance is currently recognized as being one of the most influential processes operating on community structure (e.g. Paine and Levin, 1981, Petraitis *et al.*, 1989).

The fairly recent invasion of *Mytilus galloprovincialis* to the South African coastline has become a subject of interest because of its effect on the distribution of indigenous species and more broadly, on intertidal community structure (e.g. Hockey and van Erkom Schurink, 1992; Bustamante, 1994). Its success has been ascribed to its incredibly high fecundity and its ability to resist physiological stresses such as desiccation (see Griffiths *et al.*, 1992; Hockey and van Erkom Schurink, 1992). Several studies have investigated the biology and physiology of *M. galloprovincialis* under a range of environmental conditions (van Erkom Schurink and Griffiths, 1991; Hockey and van Erkom Schurink, 1992), but none have addressed its population structure in relation to environmental parameters.

The focus of this study was to first describe and quantify various aspects of population structure of *M. galloprovincialis* - including mussel cover, mussel density, size and recruit density - in relation to the physical effects of wave exposure and tidal height. This was conducted at two localities on the west coast of South Africa (Camps Bay and Groenrivier), where this mussel has achieved its highest density (van Erkom Schurink and Griffiths, 1990). The next principle objective was to determine how recruitment, and growth and mortality contribute to the population patterns detected. The Camps Bay study site was targeted for this component of the study. Finally, the effect of disturbance was investigated after winter storms caused extensive damage in the wave-exposed, low-shore area of Camps Bay, but left the exposed high-shore site and both sheltered sites relatively unaffected. Of special interest was whether the strength of byssal attachment varied between sites, between individuals situated within the extant mussel bed and on its edges, and whether any temporal variability in attachment strength occurred. The relative contribution of growth and mortality rates or recruitment and disturbance on population patterns is not known and provides an exciting opportunity for further research.

Table of Contents

CHAPTER 1

What biological patterns exist in mussel populations

under different conditions of wave exposure and in relation to zonation?

INTRODUCTION

Ecologists have traditionally searched for mechanisms that govern community structure. A growing emphasis has been to describe patterns of distributions of populations and relate them to physical and biological factors (e.g. Connell, 1972, 1975; Underwood and Denley, 1984; Witman, 1987; Menge and Farrell, 1989). Out of these concerns has emerged the relatively new scientific discipline known as landscape ecology. Landscape ecology has evolved to become a multidisciplinary (or transdisciplinary) area of study that concerns itself with more than the ecology of communities - land topography and topology, edaphic or hydrographic factors have been identified as just some of the elements contributing to community structure and regulation (see for example, Zonneveld, 1990). There is an increasing perception that it is not just processes that create patterns but that patterns themselves modify processes (Turner, 1989). An example of this is the effect that fragmentation or insularization of a habitat might have on the distribution, movement or persistence of species (Turner, 1989). Whereas fragmentation and insularization are predominantly causes for concern in terrestrial ecology, modification by disturbances is prevalent in marine ecosystems, often resulting in dramatic changes in communities. Disturbance, whether natural (e.g. storm-related) or artificial (e.g. exploitation), is undeniably one of the most important processes regulating community dynamics (e.g. Levin and Paine, 1974; Connell, 1978; Sousa, 1979, 1985; Paine and Levin, 1981; Connell and Keough, 1985; Ebeling *et al.*, 1985; Witman, 1985; White and Pickett, 1985; Petraitis *et al.*, 1989). Disturbance ecology is currently a key subject in landscape ecology, particularly in view of its dependency on scale (Sprugel; 1991; Baker, 1992; Turner *et al.*, 1993).

A distinguishing feature of landscape ecology is its concern with the sensitivity of all processes and patterns to scale (Turner, 1989; Turner *et al.* 1989; Meentemeyer, 1989; O'Neill *et al.*, 1991; Steele, 1991; Stoms, 1992; Wiens, 1992; Wiens *et al.*, 1993). Processes operate not only at different spatial scales but are also dependent on temporal scales, which range from an ecological to an evolutionary time frame (see Meentemeyer, 1989; Levin, 1992). Communities are structured by a hierarchy of processes which are reflected at different spatial and temporal scales (see Allen and Starr, 1982). By way of example, biotic interactions such as competition and predation may determine the distribution of intertidal animals on a local scale whereas on a regional scale this is brought about by recruitment rates and oceanographic features. It follows that the scale of the investigation influences the patterns one perceives (see Wiens, 1989; Levin, 1992) and there is a need for this to be addressed when recounting the underlying mechanisms. Patterns and processes may be hidden at finer scales because of an "averaging" effect at larger scales (Risser *et al.*, 1983). Similarly, patterns and processes operating at broader scales may be overlooked when the focus of a study is on a finer scale. A central issue revolves around the problems of extrapolating across

different scales (Turner *et al.*, 1989; Wiens *et al.*, 1993). These problems are exacerbated by the nonlinear nature of many abiotic and biotic processes and their interactive effects (see O'Neill *et al.*, 1991; Wiens *et al.*, 1993). Yet there is no correct scale at which to conduct scientific investigations (Levin, 1992). Rather, the appropriate scale depends on the questions asked, the organisms studied and time periods considered (see Wiens, 1989; Wiens and Milne, 1989; With, 1994).

A number of patterns and their underlying mechanisms have been recorded for intertidal shores (e.g. Connell, 1972, 1975; Underwood and Denley, 1984; Menge and Farrell, 1989). The zonation patterns of flora and fauna that are prevalent on rocky shores have been ascribed to physical and biological processes (Lewis, 1964; Stephenson and Stephenson, 1972; Connell, 1972, 1975). With increasing tidal height is a tendency for intertidal animals to experience greater heat stress and desiccation due to decreased water inundation or high insolation. The ability to withstand these stresses often determines the upper tidal level to which different species extend. Animals inhabiting high shores may also have a reduced feeding time (particularly if they are filter-feeders) which is likely to have consequences for their zonational patterns (Underwood and Denley, 1984). Additional factors affecting distribution patterns include competitors (e.g. Connell, 1961; Branch, 1984a; Branch, 1984b) and the presence or absence of predators or grazers which may influence the relative abundance of prey or algae on rocky shores (e.g. Witman, 1987). These biotic interactions operate at a relatively small scale of centimeters to meters. The supply of larvae and their recruitment have been the subject of several recent studies on distribution patterns existing in intertidal zones (Taylor and Littler, 1982; Underwood and Denley, 1984; Witman, 1987; Menge and Farrell, 1989) and may be influenced by oceanographic conditions operating at a much larger scale of tens to thousands of kilometers. The magnitude of wave exposure also influences the biology and ecology of intertidal organisms (Jones and Demetropoulos, 1968; Witman, 1987; Menge and Farrell, 1989). Abundance may be determined by the degree of wave exposure, for a number of reasons, including physical stress and disturbance, associated changes in food availability or differential recruitment rates. Organisms persisting in areas of heavy wave action often achieve greater sizes because of increased nutrient or food uptake. Hydrological forces of a given nature and magnitude are experienced quite differently by animals of different sizes and shapes and this in turn can determine their persistence in a particular environment (Denny, 1988). The magnitude of wave exposure and tidal elevation are, in fact considered to be amongst the most important local physical gradients in intertidal habitats, and are responsible for the observable patterns that emerge at an intermediate scale of centimeters to hundreds of meters (Menge and Farrell, 1989).

The main objective of this study was to compare what patterns in mussel cover and density, mussel size and recruitment emerge from variation in wave exposure and shore height at two locations on the west coast of South Africa - Camps Bay and Groenrivier. The mechanisms thought to create these patterns are examined at a later stage in the thesis. Mussel population demography at the Camps Bay sites are compared with sites at Groenrivier to determine similarities that may reflect environmental conditions occuring there.

MATERIALS AND METHODS

Preliminary visits to both Camps Bay and Groenrivier (Figure 1.1) were undertaken to identify suitable study sites. Areas experiencing different degrees of wave exposure were selected on the basis of wave action and not on a biologically-defined indicator (e.g. Ballantine, 1961) which would have incurred a circular argument. Observations at these sites revealed that there is extensive variability in mussel cover, sizes of animals and recruitment which appeared to be related to wave action and shore height. These elements were then quantified under contrasting conditions of wave action and at different heights on the shore.

1 Localities

1.1 Camps Bay

The exposed area identified at the Camps Bay site constitutes a steeply sloping, jutting rock that experiences strong wave action. Just adjacent to this, is a sheltered bay with less of an incline and milder wave action. These two areas were targeted as sites experiencing biologically relevant, dissimilar wave action (see Figure 1.1). Camps Bay was sampled in the first week of February, 1993.

1.2 Groenrivier

Three areas were identified as suitable research sites that would allow comparisons to be made with regard to wave action. A prominent finger of rock experiencing heavy wave action contrasted with a very sheltered bay comprising seaward boulders and a stretch of quite level landward rock. Between these two areas is a section of shore having a gradient of wave exposure lying between the two extremes (see Figure 1.1). Bustamante (1994) measured wave force at these sites, simultaneously, with a simple dynamometer. The maximum force recorded for the exposed zone was 15 000 Nm^{-2}, for the semi-exposed zone was 7 000 Nm^{-2} and for the sheltered was 1 500 Nm^{-2}.

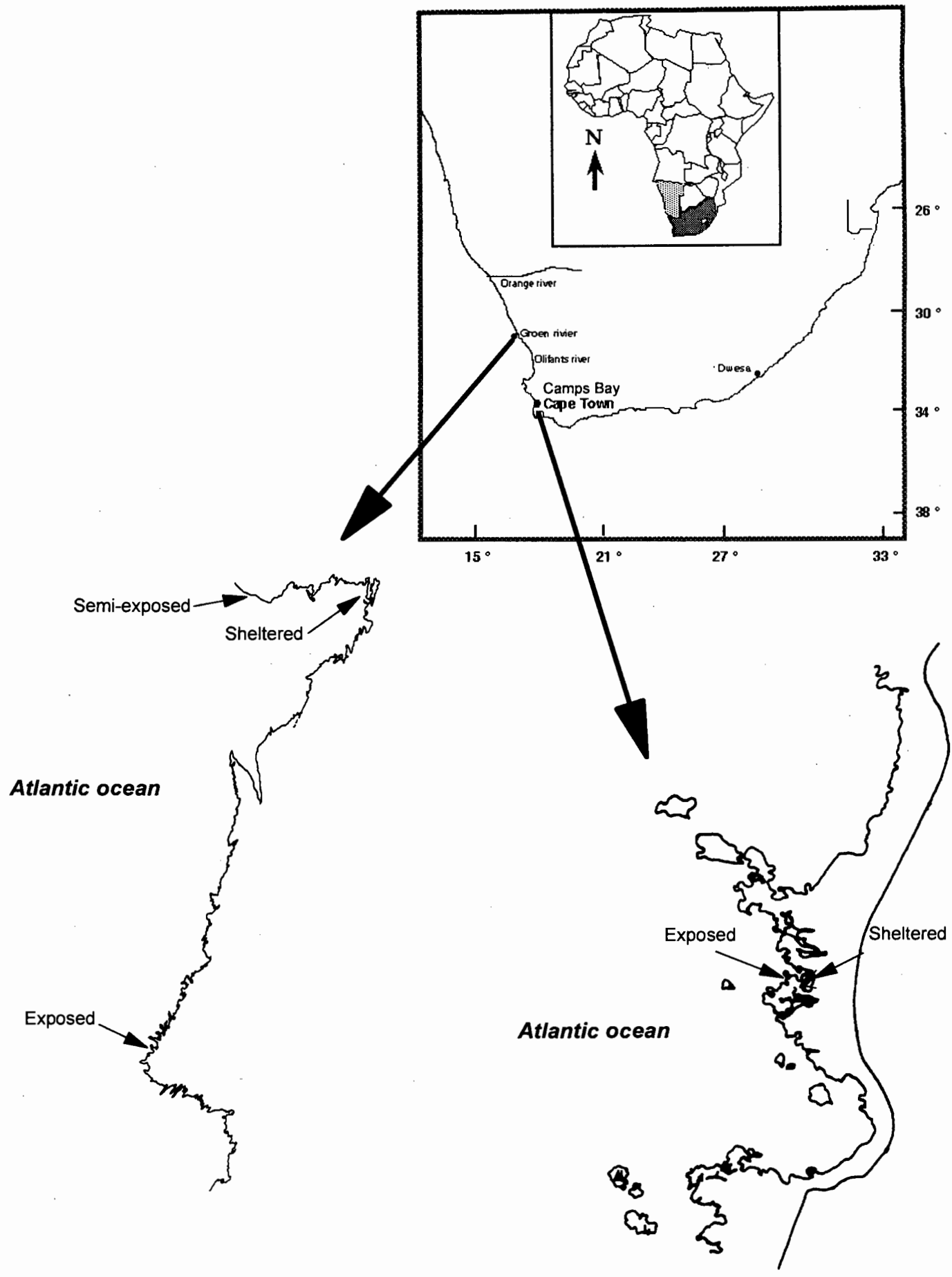


Figure 1.1 Rough map showing the relative position of the two study sites, and the location of the experimental areas at each site.

Data for the present study were collected from Groenrivier in the last week of January, 1993.

2 Measurement of mussel cover

Sites experiencing differing grades of wave action, selected at Camps Bay and Groenrivier, were sampled to establish the effect of wave exposure on intertidal mussel cover. At each site, three transects were mapped vertically up the shore, running from low water spring tides (LWST) to the upper limits of mussel distribution. Samples were based on 0.5 m^2 quadrats. String was tied to the frame of the quadrat at 5 mm intervals along its length and breadth, creating a grid of 171 intersecting points used to score mussel cover. Five quadrats were placed sequentially and approximately equidistantly on each transect line so that the effect of shore height could be determined. All sampling was conducted during spring tides.

For Camps Bay, a two-way ANOVA (SYSTAT v 5.0) was performed on mussel cover for the categories zone (sheltered and exposed) and height (low, mid-low, mid-shore, mid-high and high).

The relationship between mussel cover and wave exposure/shore height at Groenrivier was analyzed similarly, the only difference being that three grades of exposure (exposed, semi-exposed, sheltered) were compared.

3 Density of mussels

Mussel abundance is not related to percentage cover in a simple manner because mussel beds on the low shore are often multilayered and mussels higher up the shore are smaller, so more of them could potentially be packed a given area. Separate destructive samples were therefore taken for analyses of density, size composition and recruitment. Camps Bay was sampled for the week starting from the 30th July to 1st August 1992. The exposed and semi-exposed areas at Groenrivier were sampled on the 26th August 1992 while the sheltered area was visited on 20th January 1993.

As with the previous data collection for mussel cover, three transect lines were mapped at each site. Five small quadrats (25 x 25 cm) were placed approximately equidistantly along each transect from LWST to the upper limits of mussel zonation, and mussels within a quadrat were removed with a paint scraper. Mussels of all sizes were collected and the length dimension was selected to indicate size. Initially, the mussels were manually counted and measured to the nearest millimeter with vernier calipers. However, the majority of samples were counted and measured a the Joyce-Loebl (micro-magiscan 3) image analyzer and M3Genias software package.

The Joyce-Loebl image analyzer comprises a computer with a central processing unit designed specifically to analyze images (as opposed to mathematical operations). In addition to having a normal peripheral computer screen (which enables one to interact with the software package), the computer is connected to a second screen, linked to a camera lens via cables. Two camera lenses were used, depending on the size of mussels being measured: a 16 mm F1.4 Cosmicar lens was used for large mussels and a Pentax smc pentax-f 50 mm macro lens for smaller animals. Mussels were aligned on a light box directly underneath the camera lens so that their image was not distorted on the screen. The image can then be converted into digital format, saved and analyzed. Each image is calibrated to allow the computer to convert the number of pixels that each "mussel" constitutes into any required unit of measurement, e.g. length. The advantage of this method is that several mussels (sometimes hundreds) may be measured at the same time if captured in one image. The measuring operation takes no more than a minute to complete and counts of mussels and their lengths are recorded simultaneously in a computer file.

Two-way ANOVA's (SYSTAT v 5.0) were employed to determine where significant differences in mussel abundance occur with respect to wave action and tidal height.

4 Density of recruits

The association between recruit abundance and wave exposure or tidal elevation was investigated at both Camps Bay and Groenrivier; recruits were defined as young mussels within the 0 - 15 mm size range. A two-way ANOVA (SYSTAT v 5.0) was performed on data which were derived from the size-frequency analyses described above.

5 Size of adults

The size composition of adult mussels (> 15 mm in length) was quantified at both Camps Bay and Groenrivier. The data collection for these analyses has been described in section 3, above: all mussels were measured with the Joyce-Loebl image analyzer.

A two-way ANOVA (SYSTAT v. 5.0) was executed on the length data for both Camps Bay and Groenrivier in relation to wave action (sheltered and exposed for Camps Bay, sheltered, semi-exposed and exposed for Groenrivier) and tidal height (low, mid-low, mid-shore, mid-high and high).

ANOVA's for Camps Bay and Groenrivier were repeated for the maximum lengths attained by animals in each replicate at each site, because the large numbers of small adults (e.g. 15 - 45

mm) would affect the overall patterns of sizes of older adults. ANOVA's were run on untransformed data after testing for homogeneity of variances.

6 Population patterns at Groenrivier and Camps Bay

Length-frequency data collected from Camps Bay and Groenrivier (see section 3 above) were used to perform hierarchical cluster analysis and non-metric multidimensional scaling (MDS) using the PRIMER v 4.0 beta statistical package. Mean densities of each size class were calculated for each site (at each locality), experiencing different grades of wave exposure and at varying tidal heights. All analyses were performed on fourth-root transformed data and are based on the Bray-Curtis similarity index.

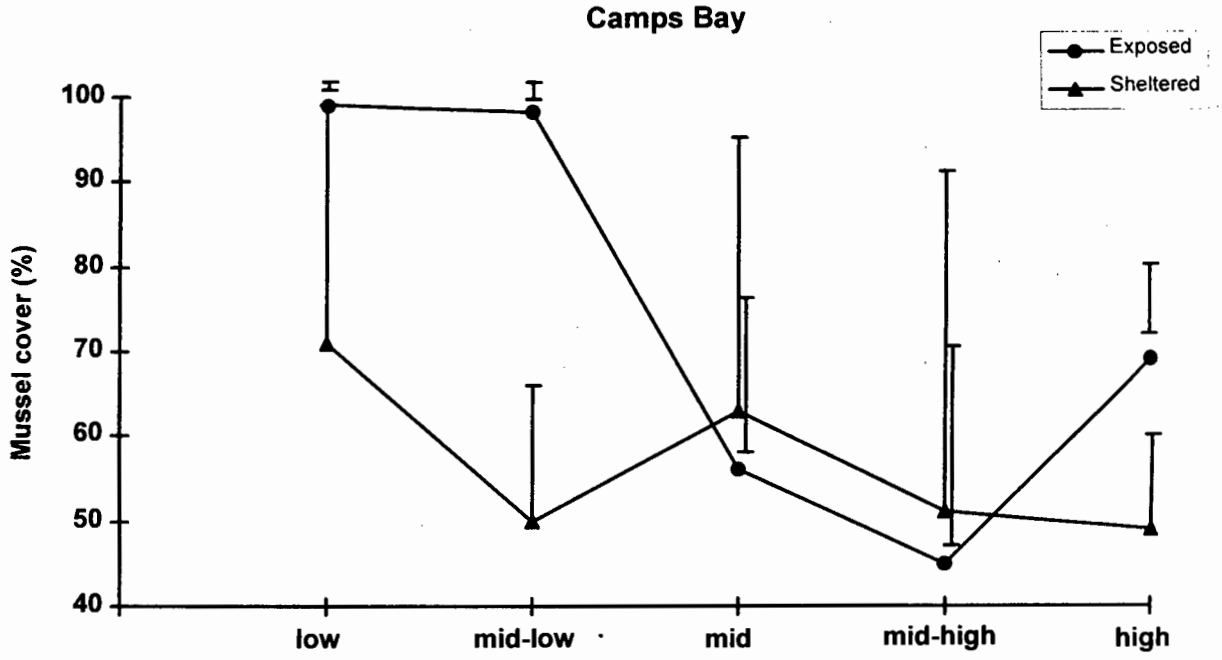
RESULTS

1 Mussel cover

1.1 Camps Bay

Mussel cover for the Camps Bay study site is illustrated in Figure 1.2., from which obvious differences between the sheltered and exposed areas can be seen. On average, the amount of cover for these areas was 57% and 73% respectively. In the sheltered zone, mussel cover gradually declined with shore height, from 71% in the low shore to 49% in the extreme upper shore, although it was fairly high in the midshore (63% cover). While this trend was evident in the exposed zone, the amount of cover on the high shore was unexpectedly high (69%).

M. galloprovincialis cover was statistically greater in the exposed area than in the sheltered area (ANOVA, $n = 30$, $\alpha = 0.05$, $p < 0.05$). Additionally, mussel cover varied significantly with height on the shore ($p < 0.05$) . An *a posteriori* Bonferroni multiple comparisons test revealed that this result was attributable to differences between the low zone and the mid-high zone (experimentwise $\alpha = 0.05$, $p < 0.05$). No other differences were statistically significant ($p > 0.3$), nor was there an interactive effect ($p > 0.1$).



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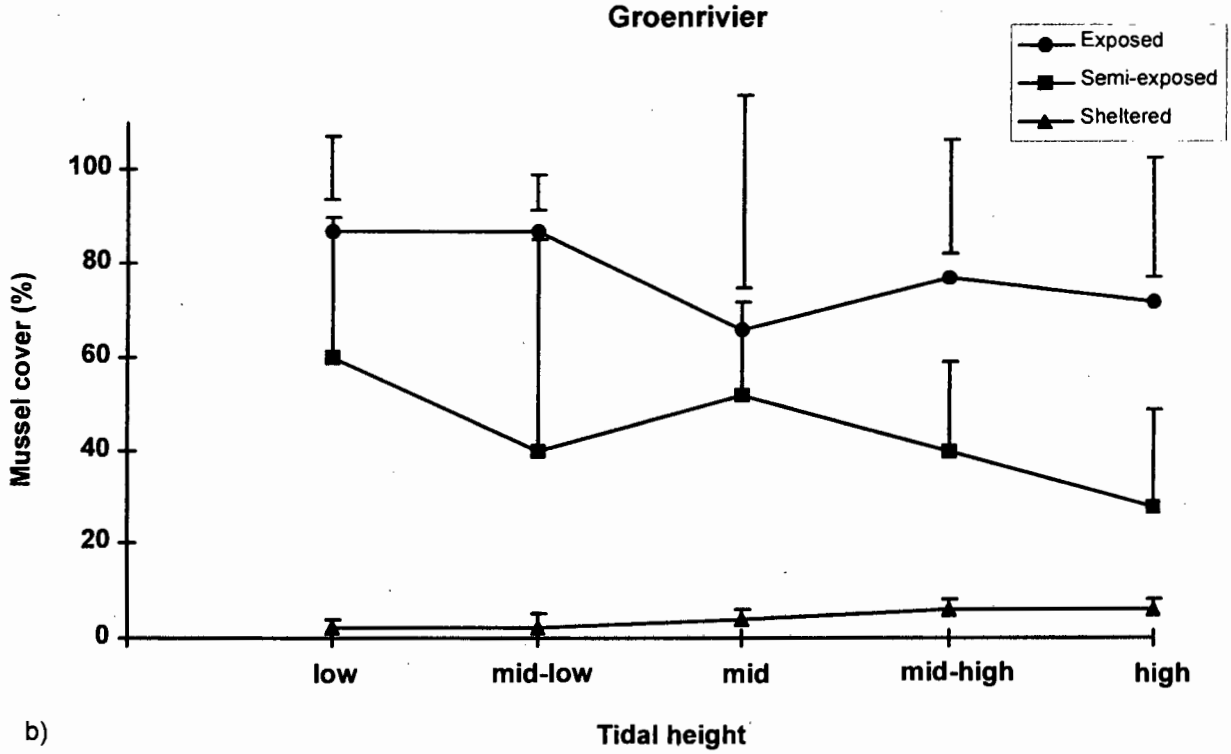


b)

Figure 1.2 Mussel bed cover at Camps Bay and Groenrivier at different grades of wave action and at different tidal heights. Data points are the means obtained from three replicates each and standard deviations are illustrated by the vertical lines with bars. S.D.'s of the "exposed" data are displaced for easy reference.

1.2 Groenrivier

The amount of mussel cover for sheltered, semi-exposed and exposed areas for Groenrivier are graphed in Figure 1.2. Mussel cover declined rather dramatically with wave exposure; while the exposed zone experienced an average cover of 78%, this dropped to 45% in the semi-exposed region and was sparse in the very sheltered bay (4%, on average). The general zonational trend for both exposed and semi-exposed areas was for *Mytilus* cover to decline upshore. In the semi-exposed area, mussel cover declined from 60% in the low intertidal to 28% furthest upshore but the midshore zone peaked at 52%. This pattern reflects the trend obtained at the Camps Bay sheltered area. By comparison, mussel cover in the sheltered zone increases gradually with tidal height, from 2% cover (on average) to 6%.

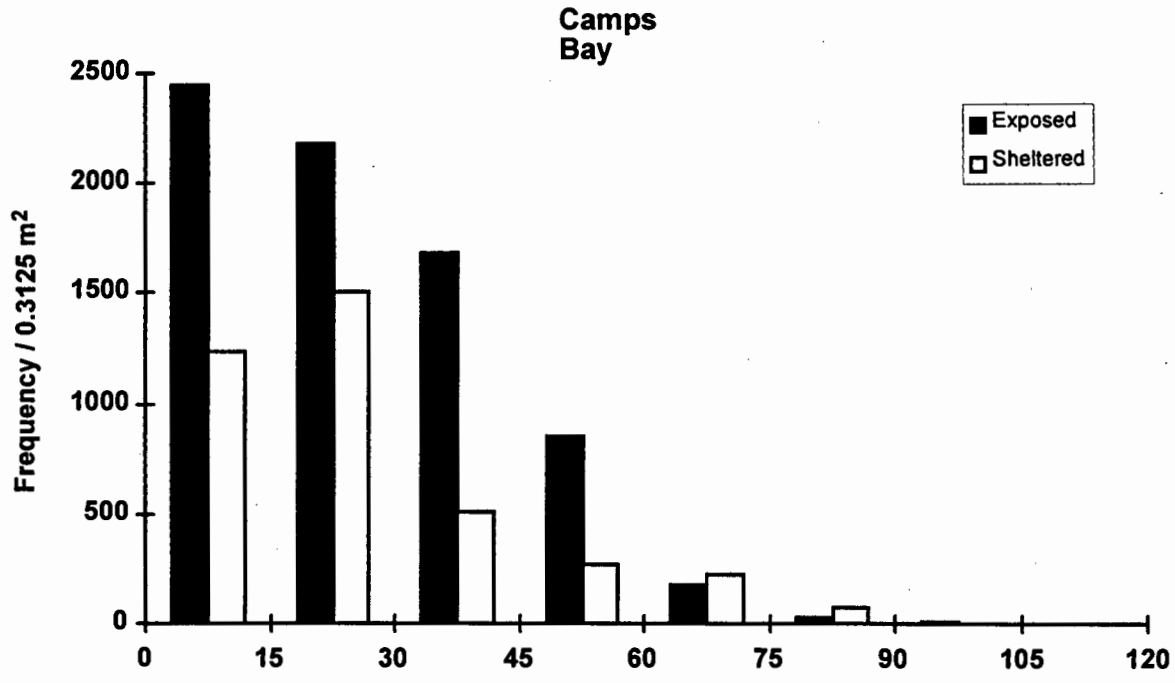
The analysis of variance confirmed that mussel cover increased significantly with the degree of wave exposure ($n = 44$; $\alpha = 0.05$, $p < 0.001$). A Bonferroni post hoc comparisons test indicated that the three sites are all significantly different to one another (experimentwise $\alpha = 0.05$, $p < 0.001$). No statistical differences regarding height on the shore were detected ($p > 0.6$), nor were there significant interactive effects ($p > 0.8$).

2 Density of mussels

2.1 Camps Bay

Data for Camps Bay are presented as length-frequency histograms in Figure 1.3, from which patterns of mussel density at different grades of wave action can be derived. Densities for each 15 mm size class were generally far greater in the exposed area than the sheltered area. The exposed area (on the whole) had a total of 7 368 mussels per 0.3125 m^2 area; about twice that of the entire sheltered area, which had 3 814 individuals in the same area. Mean densities for the sheltered and exposed areas, at the tidal levels sampled, plotted in Figure 1.4. reveal the same pattern of increased density with wave exposure. An unexpected trend of increasing density with tidal elevation exists for both sheltered and exposed areas. The mid-high zone of the sheltered area had the greatest mean density for this area (503 animals per 0.0625 m^2)

The density of mussels occurring at the wave-exposed site was statistically greater than the sheltered site (ANOVA, $n = 30$, $\alpha = 0.05$, $p < 0.05$). However, density was not significantly influenced by shore height ($p > 0.1$), nor were there interactive effects ($p > 0.5$).



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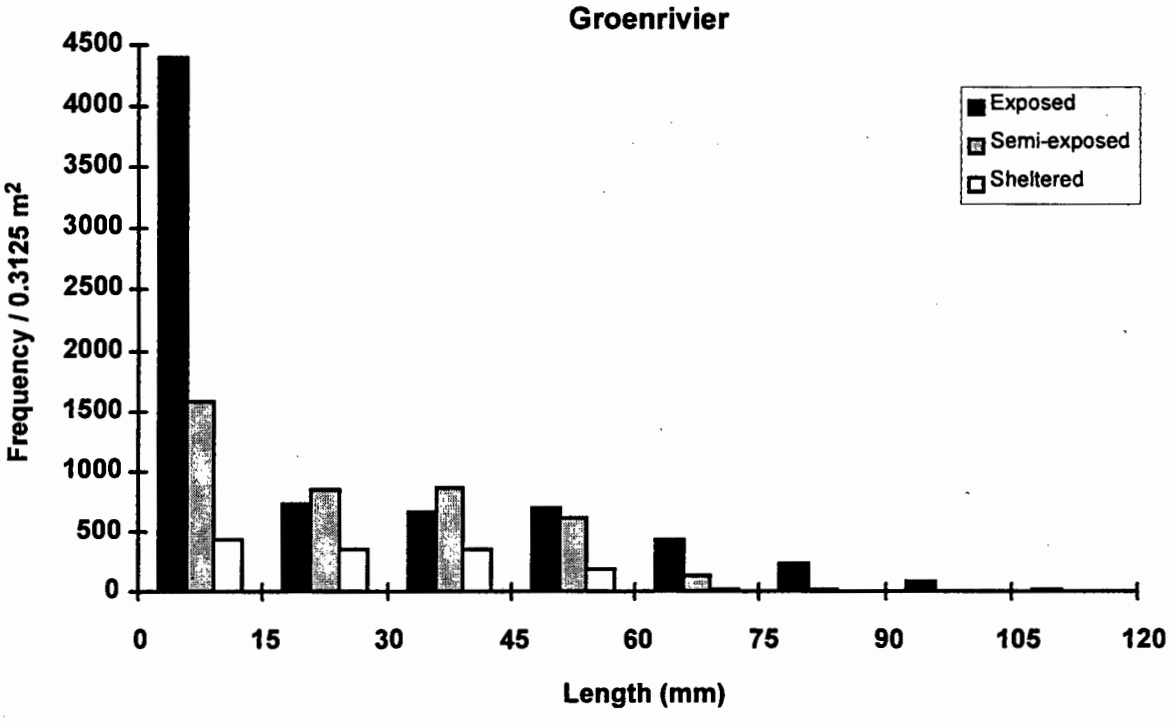

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Figure 1.3 Length-frequency plot for Camps Bay and Groenrivier at areas experiencing different grades of wave action. Data from each tidal height have been combined.

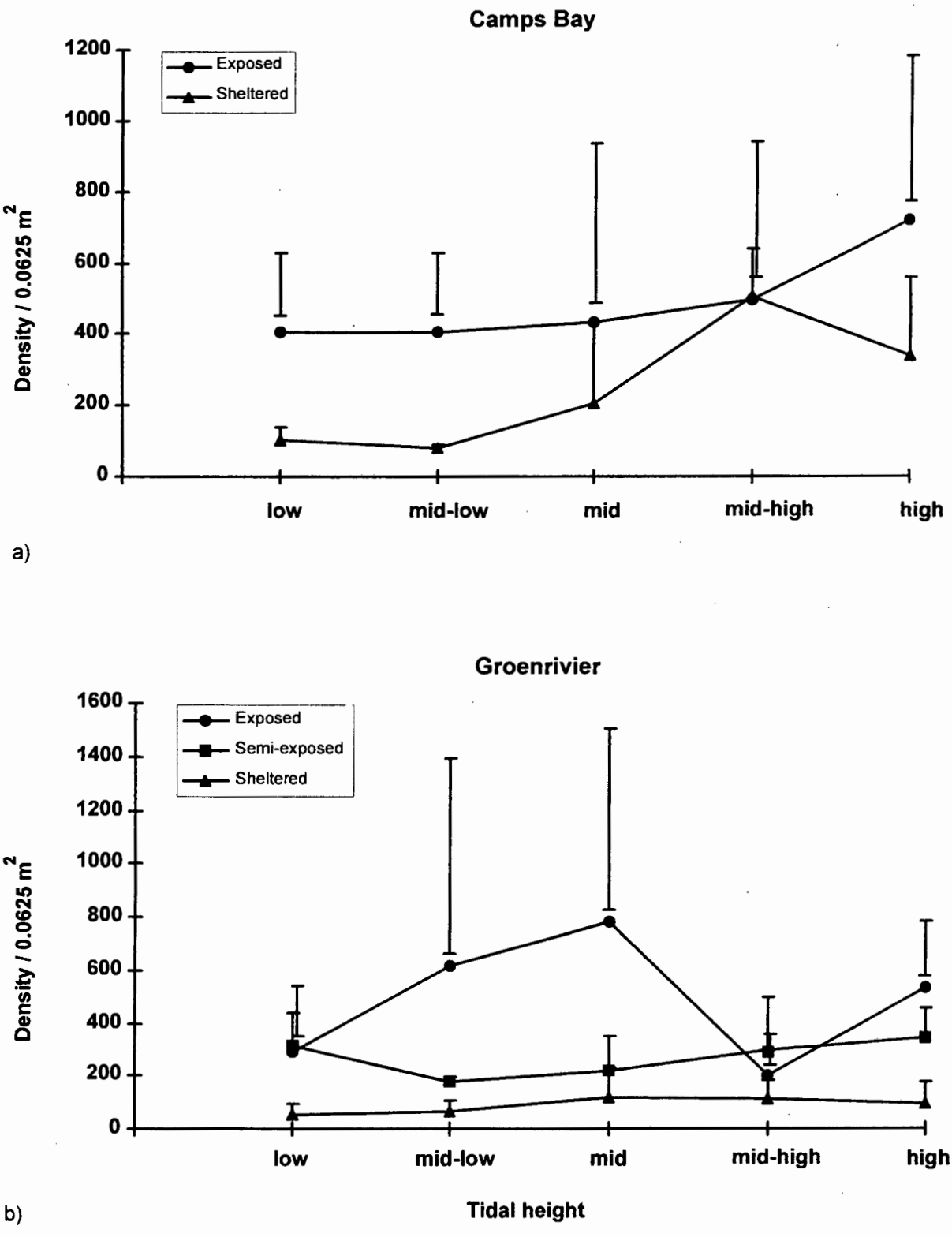


Figure 1.4 Mean densities of mussels at Camps Bay and Groenrivier from wave-exposed areas and more sheltered areas, at each tidal height sampled. Vertical lines with bars indicate standard deviations. S.D.'s of "exposed" are displaced for easier reference

2.2 Groenrivier

As with Camps Bay, density of mussels in the exposed area at Groenrivier was notably greater than in less exposed areas (Figure 1.4). Density declined from an average of 485 mussels (per 0.0625 m^2) in the area experiencing heaviest wave action, to 271 mussels/0.0625 m^2 in the semi-exposed zone and to a mere 89 individuals/0.0625 m^2 in the very sheltered zone. The difference in total densities between the exposed and sheltered areas was more extreme than for Camps Bay - more than five times as many mussels were found at the Groenrivier exposed area (7 277 mussels/0.3125 m^2) than the most sheltered area (1339 per unit area). Interestingly, the density of mussels in the exposed area at Groenrivier is comparable to density at the Camps Bay exposed zone, and the semi-exposed area at Groenrivier has only slightly more mussels per unit area than the Camps Bay sheltered area (4063 mussels per unit area for Groenrivier versus 3814 for Camps Bay). These similarities may reflect similar environmental conditions between the two exposed areas, and between the semi-exposed area at Groenrivier and the sheltered area at Camps Bay.

The relationship between zonation and mussel densities is not consistent for different grades of wave action at Groenrivier (Figure 1.4). Densities tended to increase with tidal elevation in the sheltered and semi-exposed areas, but fluctuated dramatically in the most exposed area. High densities in the mid-low and mid regions of the exposed area are probably attributable to exceedingly high recruit densities in these zones (see section 3 later).

The length-frequency distribution for Groenrivier (Figure 1.3) indicates a vast difference in recruit densities between areas experiencing differing grades of wave exposure - recruitment increased with increasing wave action. However, not all size classes exhibit this pattern. Densities of larger mussels in the semi-exposed area tended to be greater than in the exposed area, and densities of all size classes of both areas exceeded that of the sheltered area.

The ANOVA confirmed that the values obtained at the different wave-exposure sites were significantly different ($n = 45$, $\alpha = 0.05$, $p < 0.01$). Height on the shore did not produce a significant effect ($p > 0.5$), nor was there an interactive effect between categories ($p > 0.5$). A Bonferroni post hoc comparisons test ($\alpha = 0.05$) found that mussel abundance at the exposed area was significantly greater than the sheltered area ($p < 0.01$). The semi-exposed area did not differ from either of these zones ($p > 0.1$).

Despite the lack of statistical significance of shore height on mussel density, the overall trend at both Camps Bay and Groenrivier was for density to be greater in the high shore than the

low shore, even though the percent cover by mussels showed the reverse trend. This pattern was clear at all sites, with the exception of the sheltered site at Groenrivier where mussel cover increased upshore (from 2% to 6%).

3 Density of recruits

3.1 Camps Bay

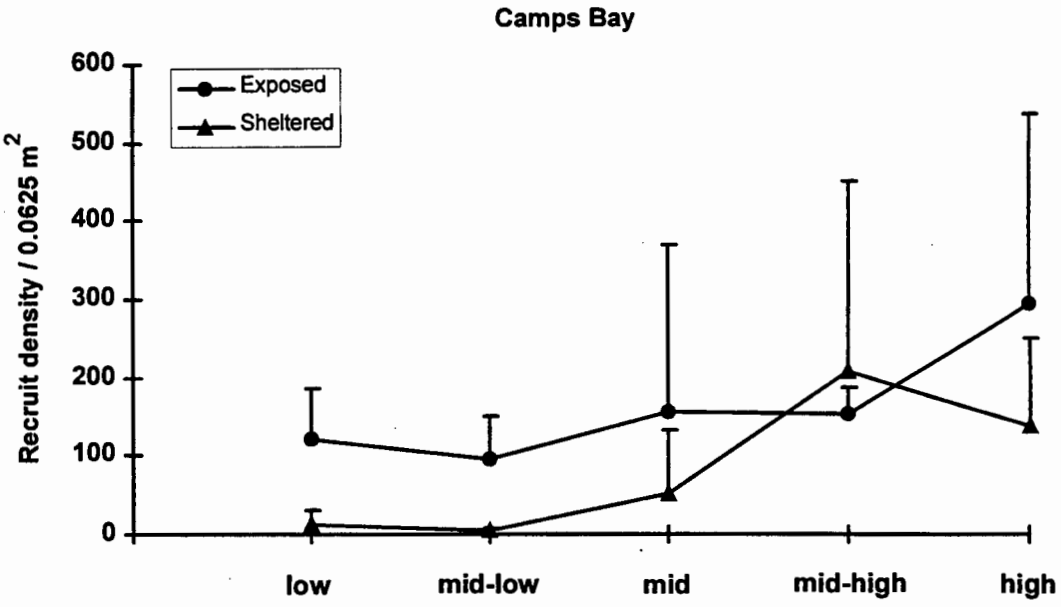
Approximately twice as many recruits (0 - 15 mm) occurred in the wave-exposed area than the sheltered area (see Figure 1.3). Total densities for these areas were 2449 recruits per 0.3125 m^2 and 1239 recruits per 0.3125 m^2 respectively. There was also a trend for the density of recruits to increase from the low to the high shores (Figure 1.5). On average, over twice as many recruits were found at the exposed high site (293 recruits / 0.0625 m^2) than at the exposed low site (121recruits / 0.0625 m^2). In the sheltered bay the difference between the extreme lower and upper sites was more pronounced and the greatest difference was between the mid-high site and the lowest site (208, versus 12 recruits per unit area).

The two-way ANOVA performed on all replicates produced unexpected results - neither height nor wave exposure produced significant effects ($n = 30$, $\alpha = 0.05$, $p > 0.1$). No interactive effects were detected ($p > 0.5$).

3.2 Groenrivier

Density of recruits declined markedly with wave exposure at this study site (Figure 1.3). The sheltered site had a modest total of 440 recruits (0.3125 m^{-2}) compared with 1584 (0.3125 m^{-2}) in the semi-exposed zone. Recruit density increased to 4406 (0.3125 m^{-2}) in the exposed area, creating a tenfold difference between the two extremes. In the sheltered area, recruit density tends to increase upshore, mirroring the pattern detected for both exposed and sheltered areas at Camps Bay (Figure 1.5). There was no firm trend for either the semi-exposed region or the exposed region at Groenrivier. Recruit densities peaked in the mid-low and mid shore levels in the exposed area - mean densities for these sites were comparable, reaching 493 and 520 per 0.0625 m^2 respectively.

The ANOVA established that recruit density did not vary significantly with shore height ($n = 45$, $\alpha = 0.05$, $p > 0.5$) but did vary with different grades of wave exposure ($p < 0.05$). The Bonferroni post hoc test ($\alpha = 0.05$) comparing exposed and sheltered sites found these to be different ($p < 0.05$). No other differences were statistically significant ($p > 0.1$).



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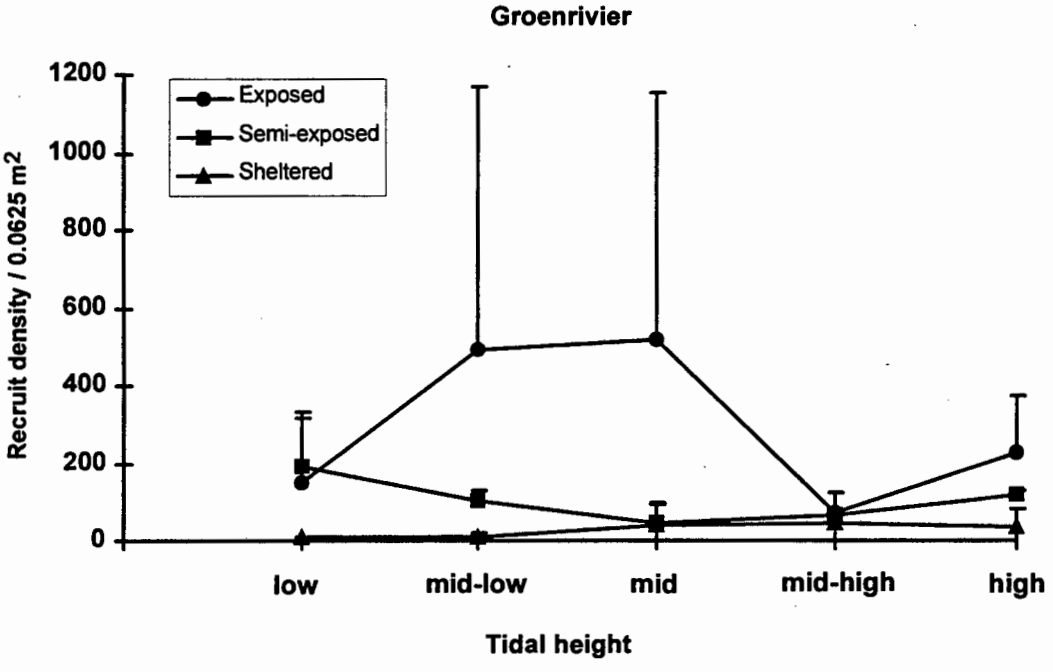

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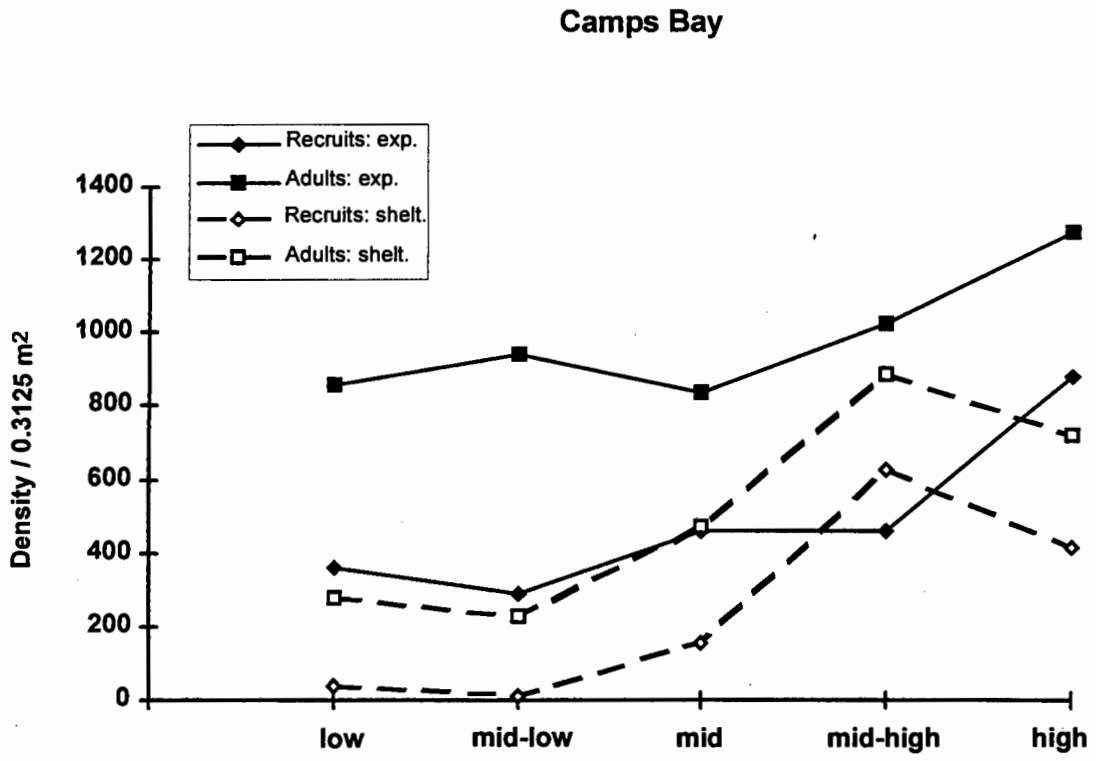
Figure 1.5 Recruit densities at various tidal heights and grades of wave exposure at Camps Bay and Groenrivier. Data plotted are the means of three replicates (transects). Standard deviations are represented by vertical lines with bars.



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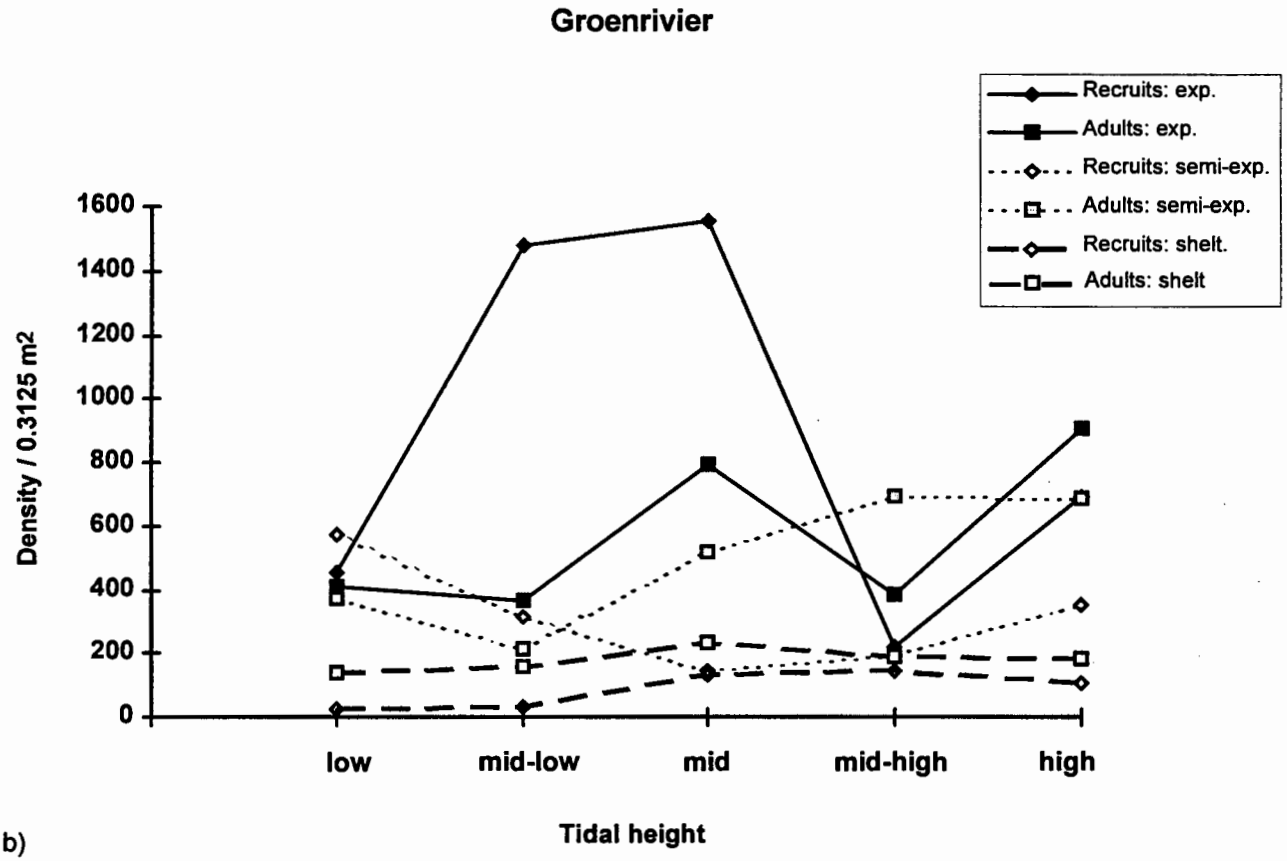


b)

Figure 1.6 Total recruit densities and adult densities at varying grades of wave exposure and at different tidal elevations for a) Camps Bay and b) Groenrivier. Exp. = exposed area, shelt. = sheltered area.

Recruit densities and adult densities are plotted in Figure 1.6. to illustrate their association on the basis of wave exposure and shore height, at both Groenrivier and Camps Bay. At Camps Bay, the association between recruit and adult densities is remarkably consistent across different tidal elevations at both sheltered and exposed areas. The same may be said for the recruit-adult association at the sheltered area at Groenrivier, but it is not predictable for th semi-exposed and exposed regions. Exceptionally high post-settlement mortality rates may be inferred at the mid-low and mid zones of the exposed area. Very low mortality rates are depicted at the mid, mid-high and high zones of the semi-exposed region. It is not whether these patterns are consistent temporally at either Camps Bay or Groenrivier. The recruit-adult density relationship at the Camps Bay study site is explored further in Chapter two and their mortality rates are examined in Chapter three of this thesis.

4 Size of adults

4.1 Camps Bay

When all adults (i.e. mussels greater than 15 mm) are considered, the average size of mussels in the exposed area was not as great as in the sheltered area (Table 1.1, bold print). This is a reflection of the relatively large number of smaller adults found in the exposed zone (Figure 1.3). ANOVA found the difference to be statistically significant ($n = 30$, $\alpha = 0.05$, $p < 0.05$); the effect of height was also significant ($p < 0.001$), and there was a significant interaction between height and wave-exposure ($p < 0.05$). Multiple comparisons tests such as Tukey HSD or Bonferroni cannot be performed in the event of a significant interactive effect (Wilkinson and Leland, 1990). Post hoc contrasts may, however, be performed and two such tests were employed to establish whether size was significantly different in the extreme lower and upper zones of the sheltered and exposed areas. In the sheltered bay, mussels were significantly smaller in the high zone ($p < 0.001$) but this was not true for the exposed shore ($0.05 < p < 0.07$).

Table 1.1 Mean (+ S.D.) length, in millimeters, of adult mussels at different wave exposures and tidal heights at Camps Bay and Groenrivier. Recruits (0 - 15 mm) are not included in these values. The averages calculated for each grade of wave exposure are given in bold.

	Camps Bay		Groenrivier		
	Exposed	**Sheltered**	**Exposed**	**Semi-exp.**	**Sheltered**
low	44 (11)	62 (3)	64 (8)	41 (21)	34 (11)
mid-low	37 (2)	56 (9)	43 (27)	43 (7)	42 (23)
mid-shore	34 (4)	48 (19)	44 (18)	41 (13)	34 (16)
mid-high	35 (4)	26 (6)	59 (8)	46 (16)	32 (15)
high	30 (4)	25 (7)	42 (4)	31 (3)	33 (16)
Average	**36**	**43**	**50**	**40**	**35**

A perhaps more meaningful comparison was made between the maximum sizes that mussels achieve, depending on wave-exposure and vertical height on the shore. The outcome of this

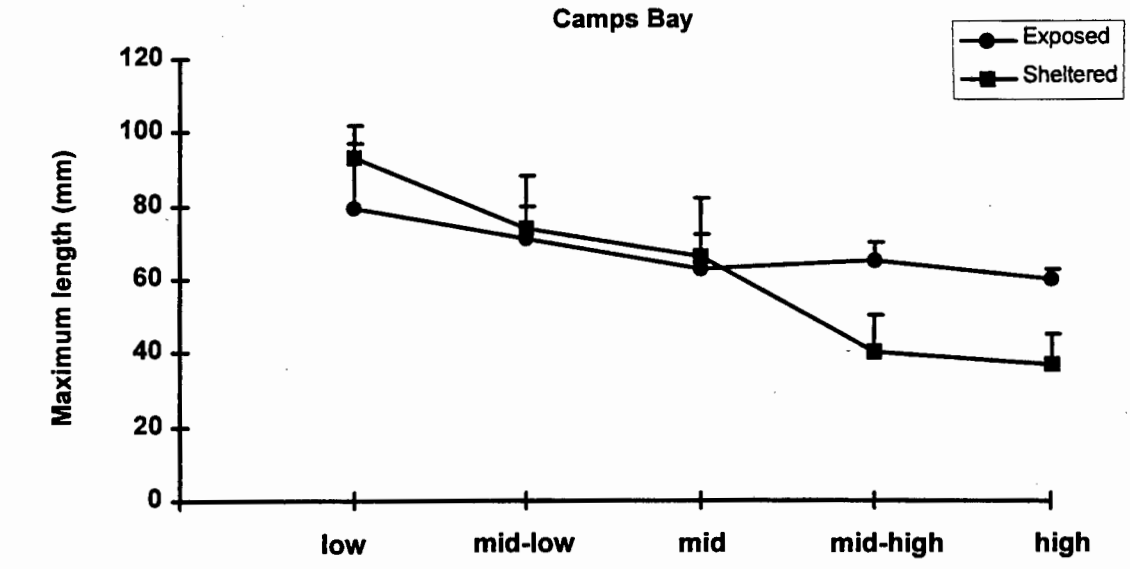
analysis was quite different to the previous analysis. Adults in the sheltered zone attain a slightly smaller maximum size than animals inhabiting the wave-exposed area (Figure 1.7). On average, mussels in the sheltered area reached a maximum size of 62 mm compared with 68 mm in the exposed area. Additionally, the maximum length that animals attain decreases with increasing shore height in both sheltered and exposed regions, as illustrated in Figure 1.7. The trend is firmer for the sheltered area.

ANOVA found that differences between the exposed and sheltered areas were statistically insignificant ($n = 30$, $\alpha = 0.05$, p 0.2). While maximum lengths were found to differ with height on the shore ($p < 0.001$), the interactive effect between the two categories was significant ($p < 0.05$). A post hoc test comparing the low and high zones in the exposed area found maximum size to vary significantly at these sites ($p < 0.05$). This was verified for the sheltered area ($p < 0.001$).

4.2 Groenrivier

The mean lengths of (all) adult mussels at Groenrivier differed with varying degrees of wave action (Table 1.1). There was a general trend for size to increase with increasing wave exposure, from 35 mm in the most sheltered area to 50 mm in the exposed area. Mean length of adults in the semi-exposed area lay inbetween these values, at 40 mm. A further result is that mussels inhabiting the low shore tended to be larger than those on the high shore. This pattern is obvious for the exposed and semi-exposed regions, but differences were insignificant in the sheltered zone. While differences between the two extremes (high and low shores) do exist for the exposed and semi-exposed area, there was no *general* trend with respect to increasing height on the shore. The ANOVA performed on this data set excluded height on the shore as a significant factor ($n = 45$, $\alpha = 0.05$, $p > 0.3$). Contrarily, mean lengths did vary significantly with wave exposure ($p < 0.01$). Bonferroni's pairwise comparisons test established that this result was attributable to a significant difference between the sheltered and exposed zones only (experimentwise $\alpha = 0.05$, $p < 0.01$).

The maximum size that mussels grew to in the exposed area was (on average) 90 mm compared with 67 mm in the semi-exposed area and 54 mm in the sheltered bay. Figure 1.7 illustrates the general tendency of maximum size to decrease with increasing shore height in the exposed area, although mussels achieved relatively high lengths in the mid-high zone. No firm pattern can be derived for either the semi-exposed area or the sheltered area. ANOVA was in



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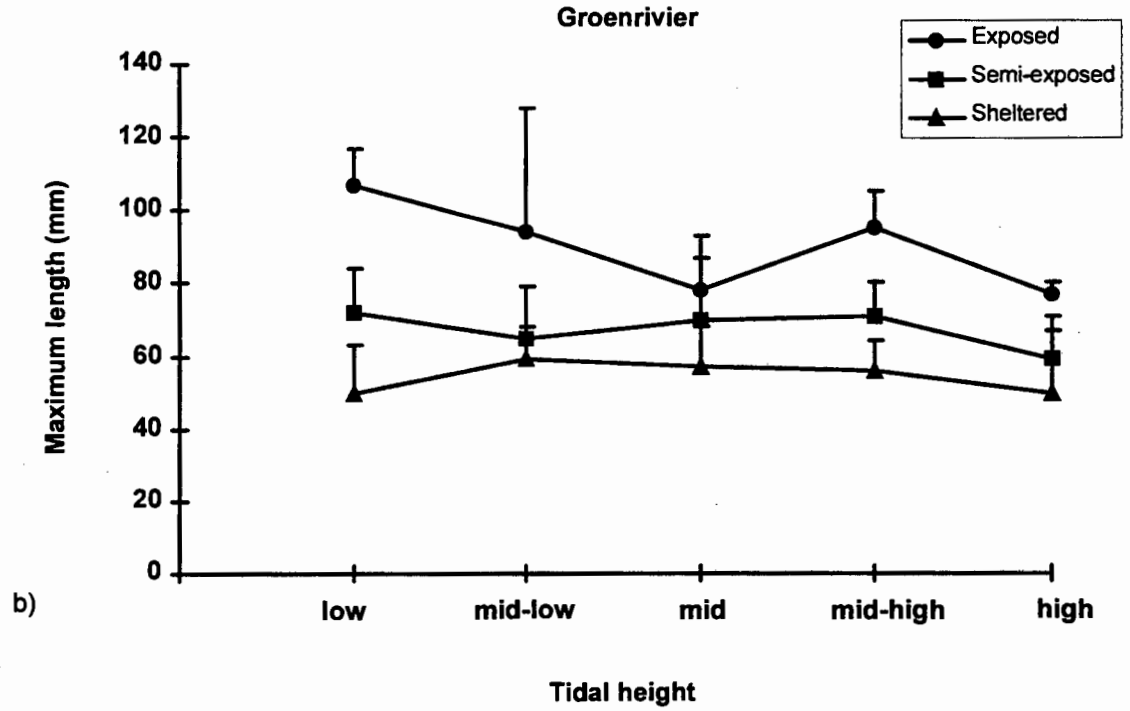


b)

Figure 1.7 Mean, maximum lengths of adult mussels at Camps Bay and Groenrivier, relative to their vertical position on the shore, for exposed and less exposed areas. Vertical lines with bars illustrate S.D.'s.

agreement with the previous analysis - differences between zones are significant ($n = 45$, $\alpha = 0.05$, $p < 0.001$) and height did not produce significant differences ($p > 0.2$). The Bonferroni pairwise comparisons test revealed that maximum lengths of animals in the exposed zone were significantly higher than either sheltered or semi-exposed areas (experimentwise $\alpha = 0.05$, $p \leq 0.001$). Differences between the sheltered and semi-exposed shores were insignificant ($p > 0.05$).

5 Population patterns at Groenrivier and Camps Bay

The hierarchical cluster analysis detected a number of very interesting population demography similarities between sites (Figure 1.8). Population size-frequency composition at the Camps Bay sheltered site was approximately 92% similar to that of the semi-exposed site at Groenrivier, a pattern that repeats similarities of mussel cover and determined for these locations (see sections 1 and 2 above). The exposed site at Camps Bay was remarkable similar to its sheltered site and the semi-exposed site at Groenrivier (91% similarity), and these sites exhibited relatively similar population demographies to the exposed site at Groenrivier (88%). The sheltered site at Groenrivier has been separated from the remaining sites (78% similarity). The separation of this site is in accordance with differences in mussel bed cover and densities between this site and other Groenrivier sites reported earlier (sections 1 and 2).

The MDS ordination plot (Figure 1.9), which reduces the similarity matrix to two-dimensions, mirrors the patterns reflected in the dendrogram from the cluster analysis. The short (Euclidean) distance between the Camps Bay sheltered site and the Groenrivier semi-exposed site indicates their strong similarity in population demography. These sites are arranged in close proximity to the two exposed sites. The sheltered site at Groenrivier is segregated from the remaining sites, indicating its dissimilarity in size-frequency composition. The stress coefficient for this analysis (0.00) reflects a perfect representation of the similarity matrix ranks, ensuring that there is no chance of misinterpretating the patterns (see Clarke and Warwick, 1994). The patterns that exist are most informative in that they probably reflect past or present environmental conditions at the sites sampled.

Dendrogram for hierarchical cluster analysis : Camps Bay and Groenrivier

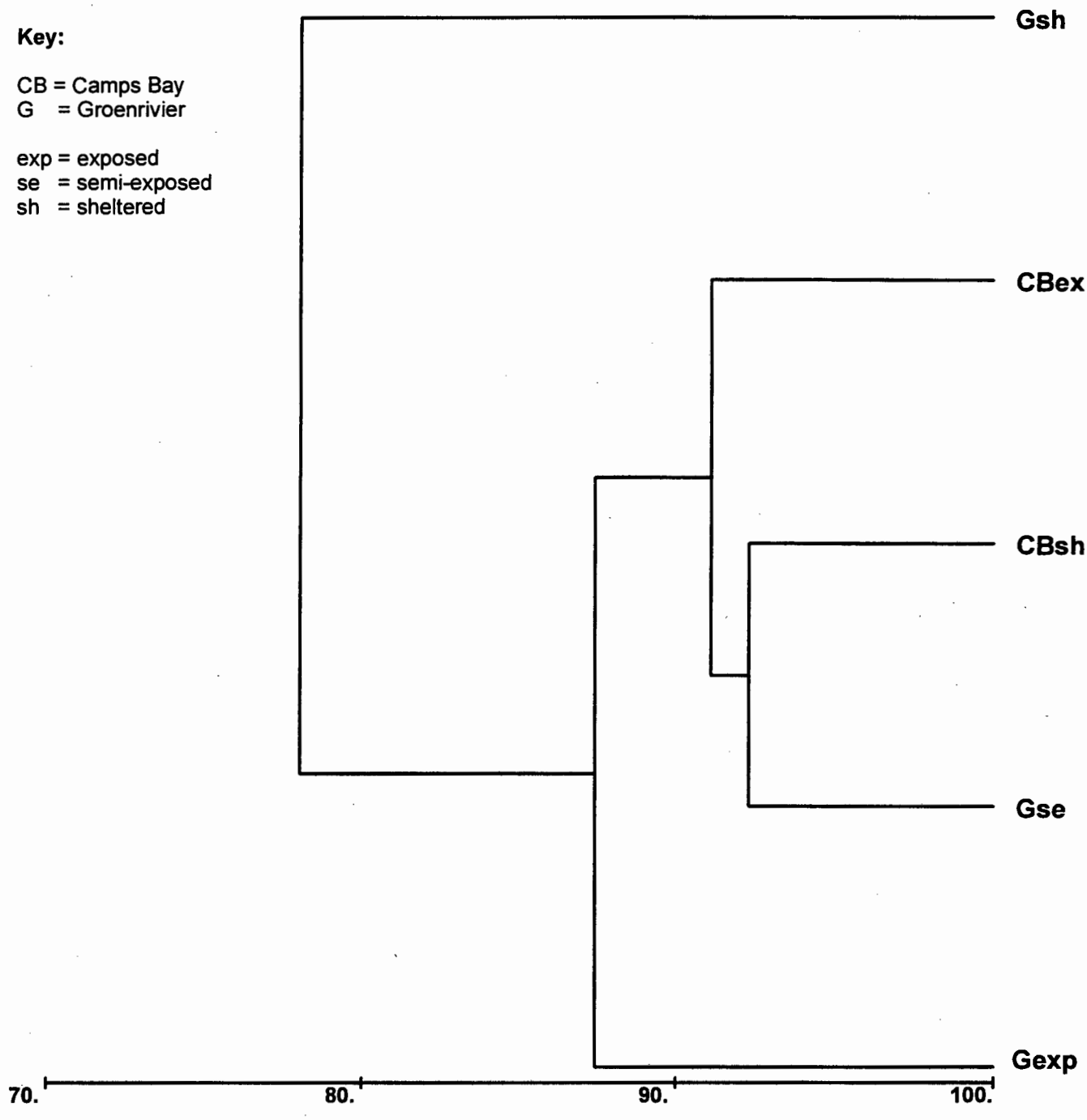


Figure 1.8 Dendrogram of hierarchical cluster analysis performed on length-frequency data from Camps Bay and Groenrivier. The configuration is plotted from Bray-Curtis similarities. Sites sampled at these localities were chosen on the basis of wave exposure. The key to abbreviations is given in the top left-hand corner of the diagram.

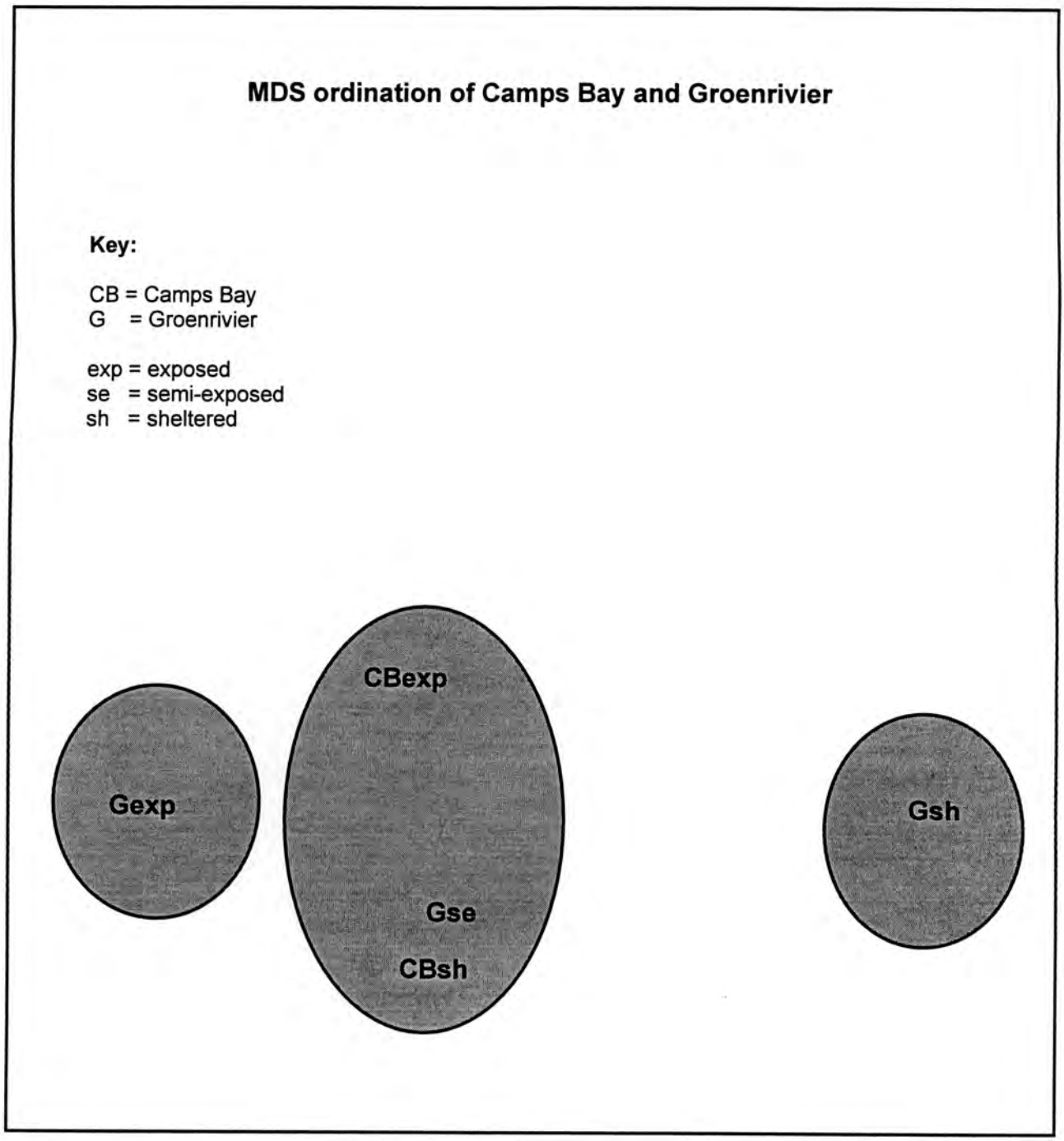


Figure 1.9 MDS ordination plot of length-frequency data for Camps Bay and Groenrivier (stress = 0.00). Data were collected from areas experiencing different grades of wave exposure. A key to the two locations and their sites is given in the diagram.

DISCUSSION

A tremendous amount of variability occurs in mussel cover, abundance and sizes of adults at different areas in the intertidal zone at Camps Bay and Groenrivier. Some of this variation was correlated with wave exposure and tidal elevation on the shore but not all of the differences that occurred were statistically significant, neither were they necessarily of a similar nature at the two study sites.

The uppermost zones of intertidal habitats are subjected to relatively high insolation and reduced periods of water inundation, which factors tend to set the upper level at which species extend and/or to negatively affect their abundance when animals are capable of withstanding the physiological stresses associated with this environment (see e.g. Lewis, 1964; Connell, 1972, 1975). As such, one would expect mussel bed cover to decrease upshore and indeed this was the general trend at the exposed and sheltered areas at Camps Bay and at the exposed and semi-exposed areas at Groenrivier. Patterns were however, obscured by the unexpectedly high mussel cover in the middle zones of the sheltered area of Camps Bay and semi-exposed area at Groenrivier and also the highest zone of the exposed area aat Camps Bay. Tidal height and wave-exposure are inextricably linked and the combination of these environmental correlates may have positively affected mussel cover in the abovementioned mid-shore zones. This does not explain the pattern exhibited at the most sheltered site at Groenrivier, where mussel cover increased slightly with increasing tidal elevation. A possible explanation may be that although wave force decreases upshore in this area (Bustamante, 1994), the differences are not marked so tidal height has little or no effect on the abundance of *M. galloprovincialis*. Statistically, tidal height had no effect on mussel cover at Groenrivier but did significantly affect mussel cover at Camps Bay.

Densities of *M. galloprovincialis* increased with increasing tidal elevation at both sheltered and exposed areas at Camps Bay and at the sheltered and semi-exposed areas at Groenrivier. While shore height had no other statistical significance, the trend described above is contrary to expectation because of the harsh environmental conditions upshore. By comparison, densities of the mytilid, *Geukensia demissa* gradually decline upshore, in accordance with seawater inundation time (Franz, 1993). However, *M. galloprovincialis* exhibits a strong resistance to desiccation (Hockey and van Erkom Schurink, 1992) which would allow them to achieve high densities in a heat-stressed environment. Additionally, animals in the higher zones attained smaller sizes than in the lower zones (Figure 1.7), so more mussels could be packed per unit area at higher shore levels. By far the most important factor to consider is the effect of recruitment on population densities. A comparison of Figures 1.3 and 1.4 reveals the striking similarities between zonational trends in recruitment densities and final mussel

densities, for all sites at Camps Bay and Groenrivier. These similarities are repeated for the recruit-adult density relationship at Camps Bay (on a whole) and for the Groenrivier sheltered bay, but high mortality rates at the exposed area and low mortality at the semi-exposed area indicate that the relationship is not spatially consistent. The influence of recruitment patterns and post-settlement mortality on adult densities are explored further in later chapters.

Although there was no statistical effect of shore height on recruitment patterns for either Camps Bay or Groenrivier, the general trend for recruitment intensity to increase upshore is counterintuitive for two reasons: 1) the period of water inundation on the high shore is reduced, so larval supply to this zone is expected to be lower and 2) recruit mortality in the high zone is expected to be greater because of thermally induced stresses (see Bertness *et al.*, 1992; Minchinton and Scheibling, 1993). While the exact relationship between settlement and recruitment of marine invertebrates remains unclear, it is noteworthy that settlement of *S. balanoides* decreased with tidal height at Rhode Island (Bertness *et al.*, 1992). In fact, settlement seems to be targeted at low tidal heights until unoccupied space becomes limited. Only then does settlement shift to tidal heights where space was available. Other possible factors that might influence recruit densities that were not covered in this investigation are the effects of biotic interactions. Menge (1991) found that recruit densities of the barnacle *Chthamalus fissus* were highest in the high shore in the presence of grazing molluscs and in the absence of predatory gastropods. It is not known whether predation or the presence or absence of grazers influence recruit abundance, or whether additional factors such as substrate type, microhabitat, space limitation or interaction with adults in the low zones at Camps Bay and Groenrivier forces mussels to recruit to higher tidal levels.

Comparisons of the maximum length attained by mussels in relation to zonation and wave action point to the dissimilarities of these effects at Groenrivier and Camps Bay. While there was a general tendency for size to decrease upshore at Camps Bay, no size differences were evident between the sheltered and exposed areas. The effects of zonation and wave action cannot be isolated statistically at Camps Bay, but an *a posteriori* comparisons test did reveal that mussels in the uppermost zone are significantly smaller than animals in the lowest zone for both wave exposures. This may reflect a reduced feeding time in the high zones which accompanies the decreased period of water inundation. In both exposed and semi-exposed areas at Groenrivier, mussels achieved a greater maximum size in the low zone than in the high zone but length and shore height were not correlated statistically. The fact that mussels in the high and low shores of the most sheltered region attained similar sizes undoubtedly swayed the results. Contrary to patterns at Camps Bay, wave-exposure clearly influenced mussel size at Groenrivier. Mussels in the exposed region attained significantly greater sizes than individuals inhabiting either the semi-exposed or sheltered zones. There is an obvious

need to measure food availability in studies of this nature as a possible cause for differences in sizes of animals, which may be associated with wave exposure and tidal elevation. It must be added that size alone reveals nothing about growth rates at different locations or under different environmental conditions - results obtained for *Geukensia demissa* indicated that shell length did not differ between tidal levels even though growth rates declined upshore (Franz, 1993). Growth rates of *M. galloprovincialis* occuring at Camps Bay are explored in Chapter three.

A final comment regarding zonation is that the effect of tidal height on the structure of mussel beds at Camps Bay Groenrivier may differ because of topographical differences: the rockface at Camps Bay inclines more steeply than at Groenrivier, with the result that the high shore and low shore zones at the former study site are more dissimilar. Distinct topographical features such as crevices were avoided but more obscure peculiarities may also have had consequences for mussel bed structure. Nonetheless, the effect of shore height cannot be expected to be linear and variability and patchiness may also have obscured more general patterns. It is impossible to include all causal factors in a survey of this nature and more importantly, the role of indirect elements is difficult to anticipate and evaluate (see Menge, 1991). In spite of this, noteworthy patterns do exist - similarities and variation are equally relevant in ecology.

Wave exposure had an important influence over patterns of mussel cover and density and recruitment of *M. galloprovincialis*. At both Camps Bay and Groenrivier mussel cover was significantly higher in wave-exposed than more sheltered areas. The semi-exposed area investigated at Groenrivier also had a substantial amount of mussel cover. In fact, the semi-exposed area was comparable to the sheltered area at Camps Bay in both mussel cover and mussel density, but there was a paucity of cover and density at the Groenrivier sheltered bay. Similarities between the semi-exposed site at Groenrivier and the sheltered site at Camps Bay probably reflect comparable environmental conditions. Hierarchical cluster analysis and MDS revealed close similarities in population demography between these sites, which strengthens the previous argument, and indeed analyses of this nature are thought to reflect environmental similarities - either historical or present (Clarke and Warwick, 1994). One possible explanation for enhanced mussel cover on wave-swept shores in is that larval supply is greater at these sites because of hydrodynamic effects. The importance of such hydrographic effects has been suggest elsewhere (McGrorty and Goss-Custard, 1991; Minchinton and Scheibling, 1993). For example, reduced densities of *Mytilus edulis* with distance upstream in the estuary of the River Exe in England are likely to be attributable to the decrease in water flow (McGrorty and Goss-Custard, 1991). Petraitis (1991) found *M.edulis* cover varied with wave-exposure outside Hockamock Head. Mussel cover was maintained at about 30% in slightly protected

and sheltered areas but only a few mussels were found at the most exposed location. This intriguing result (the opposite of what is recorded here) could be attributed to the dominance of the red alga, *Chondrus crispus* at the exposed site.

At both Groenrivier and Camps bay, densities of mussels increased dramatically with wave exposure. This pattern closely followed the association of recruit densities with wave action and it appears that total mussel densities are related to recruitment intensity. The relationship between recruit densities and adult densities was not as firm at Groenrivier, most likely because differential post-settlement mortality rates across wave exposures influence the relationship. The recruit-adult density relationship is addressed in Chapter two. The relevance of recruitment patterns on community structure and dynamics is repeatedly broached in the literature, either from a theoretical perspective (Fairweather, 1991; Fogarty *et al.*, 1991) or from a practical perspective (Taylor and Littler, 1982; Menge and Farrell, 1989; Menge, 1991; Petraitis, 1991; Bertness *et al.*, 1992). In particular, the latter approach often focuses on the relationship between recruitment density and wave-exposure. Bertness *et al.* (1992) found settlement of the acorn barnacle *Semibalanus balanoides* to be higher on wave-exposed surfaces than on wave-protected surfaces. Petraitis (1991) found no consistent differences in recruitment of *M. edulis* between sheltered and exposed locations in Maine, but in general, recruitment was higher on wave-swept shores. The general trend exhibited by *M. edulis* is in accordance with results of the present study.

The spatial patterns of mussel bed structure explored in this chapter are further addressed in the following chapters with a view to determine the processes that cause them. Specifically, growth and mortality are investigated with respect to wave exposure and zonation; the relationship between recruitment and final adult densities is examined on the basis of both spatial and temporal differences; and finally, the influence of disturbance on mussel populations is investigated, and the relative strength of byssal attachment determined to explore whether mussel attachment strength is related to environmental pressures.

CHAPTER TWO

Temporal and spatial variability in recruitment patterns, recruit-adult densities and population patterns of *Mytilus galloprovincialis* at Camps Bay.

INTRODUCTION

The trend in marine ecological literature has moved from investigating the effects of competition and predation on community structure toward evaluating the importance of settlement and recruitment processes on community or population patterns (e.g. Underwood and Denley, 1984; Gaines and Roughgarden, 1985; Sutherland, 1987; Raimondi, 1988; Menge and Farrell, 1989; Karlson and Levitan, 1990; Menge, 1991; Petraitis, 1990, 1991; Young, 1991). Settlement and recruitment of marine invertebrates are episodic events that vary both spatially and temporally (see Wethey, 1984; Menge, 1991; Michener and Kenny, 1991; Pennings, 1991; Bertness *et al.*, 1992; Turner and Todd, 1993). Such variation may be attributed to broad scale processes such as currents or other oceanographic or hydrodynamic features (e.g. Kingsford, 1990; Pineda, 1991; Snelgrove, 1994), to biologically relevant factors such as the spawning period (McShane and Smith, 1991) or to finer-scale influences such as topography, substrate type or surface chemistry (Seed, 1969; Wethey, 1984; Petraitis, 1990; Roberts *et al.*, 1991; Pawlik, 1992). Local physical factors such as wave exposure and tidal elevation also influence the processes of
settlement and recruitment (e.g. Bertness *et al.*, 1992; Turner and Todd, 1993). These processes are in turn thought to be reflected in the population structure (e.g. Gaines and Roughgarden, 1985; Davis, 1988). It is the interplay of environmental factors and recruitment variability, and their role in regulating populations that has become the focus of supply-side ecology (Butler, 1990; Fairweather, 1991; Fogarty *et al.*, 1991; Grosberg and Levitan, 1992). How recruitment translates into adult abundances is not fully understood (Fairweather, 1991), but the theoretical concerns of supply-side ecology are more and more frequently being addressed by experimental ecologists (e.g. Menge, 1991; Petraitis, 1991).

The recent invasion of *Mytilus galloprovincialis* to the South African coastline has been attributed, in part, to its incredibly high fecundity (Hockey and van Erkom Schurink, 1992). The abundance and distribution of *M. galloprovincialis* is not uniform along the length of coast (see van Erkom Schurink and Griffiths, 1990; Hockey and van Erkom Schurink, 1992). Its growth, reproduction and physiological energetics have been compared with several indigenous species of mussel under a range of conditions (van Erkom Schurink and Griffiths, 1991, 1992; Hockey and van Erkom Schurink, 1992). However, no studies to date have investigated the relationship between recruitment and abundance of this mussel under various environmental conditions. The analyses of population structure at both Groenrivier and Camps Bay (see chapter one) suggested that patterns of mussel recruitment and density are related to the degree of wave action and height on the shore. Following from this, the objectives of the present study were firstly to examine the influence of wave exposure and tidal elevation on recruitment patterns in a natural population and to determine whether these patterns varied over time. Secondly, recruitment to an aritificial substrate was investigated

under a similar range of conditions, but no temporal effect was investigated. The use of artificial collectors eliminates some of the variability that accompanies differences in substrate type or availability. Thirdly, since recent emphasis in ecology leans toward the importance of recruitment on population structure, the relationship between recruit and adult densities was examined monthly at sites which differ in wave exposure and tidal height, to determine whether it was consistent temporally. Finally, comparisons of mussel population demography were made to determine similarities between sites that may reflect past or present environmental conditions.

MATERIALS AND METHODS

Data for all analyses were collected at monthly intervals from the third week in June to the third week in September 1993 (covering the period at which settlement is most intense - unpublished data) from the Camps Bay study site (see Chapter one, Figure 1.1 and 1.2). In each instance, mussels were collected and experiments conducted at sheltered and exposed sites, and in high and low tidal zones.

1 Natural recruitment

Plots were permanently marked using cable ties attached to nails that had been driven into the granite. At each site, six replicate 100 cm^2 areas of mussel bed were removed with a paint scraper, and the mussels collected into plastic bags and kept frozen at the laboratory until they could be measured and counted with a Joyce-Loebl (micromagiscan 3) image analyzer (see Chapter one for details).

The measurements were converted to length-frequency data, with a size class of 0 - 15 mm being defined as recruits (see Chapter one). A three-way ANOVA (SYSTAT v 5.0) was performed on recruit densities for the categories month, exposure and zonation (tidal height). Data were tested for homogeneity of variances. Outliers were not removed because a) deviations were relatively small (see e.g. Wilkinson and Leland, 1990) and b) recruitment can be a stochastic and sporadic process so that deviations are real biological phenomena and not freak, unexpected events.

These data were utilized in the analysis of the recruit-adult relationship and for population analysis (below).

2 Recruitment to artificial substrate

Plastic dish scourers (having an area of approximately 276 cm^2 and mesh size of ± 3.5mm) were tied to nails with cable ties and the nails hammered into drilled holes so that the scourers lay just above the surface of the bare rock. Adult mussels leaning onto the artificial substrate were removed so there was a distance of approximately 5 cm from scourer to the nearest mussel bed. There were six replicates per site. Scourers were replaced monthly, coincidentally with samples of the natural mussel bed. Mussels settling in the scourers were counted and measured with the Joyce-Loebl image analyzer, as before.

Data were standardized (numbers of recruits/number of replicates) due to the high loss of scourers at certain sites. A two-way ANOVA tested for the effects of exposure and zonation on these data. Variances were examined and outliers were not excluded from the analysis. Time was not included as a variable because of the high loss of scourers on particular dates.

3 Recruit-adult relationship

The recruit-adult relationship was investigated at each site for the period June to September 1993 noting the samples from natural mussel beds (see section 1 above). Several linear regressions (Excel v 5.0 for Windows) were performed on the data. To determine whether any temporal effects were evident, separate analyses were conducted for each month's data from sheltered and exposed areas, low and high shores. Data for June to September were then pooled for each locality. Linear regression was performed on these data to determine the influence of recruitment on adult densities for each site over the four month period. A final analysis was conducted on data combined from all sites to determine the overall recruit-adult relationship for the Camps Bay study site over the experimental period. Normal probability plots confirmed that the data were sufficiently normally distributed.

4 Population patterns

The effects of tidal elevation and wave exposure in intertidal zones are not independent of one another. While high and low shore zones are easily identifiable as separate entities in both sheltered and exposed areas, there is a grade of wave action and tidal height from the exposed low shore to the sheltered high shore rather than distinct cut-off points. The result is that discrimination between the environmental conditions from one site to the next are not immediately apparent. The biological features (such as size, cover, recruitment) emerging from the site-specific conditions may also exhibit intermediate patterns and causes of inter-site differences are therefore difficult to interpret. However, one may obtain a graphical and quantitative description of the various sites in relation to one another, using multivariate

techniques. Size-frequency data for each location were treated as if they were species-sample data to graphically describe mussel population patterns, which presumably reflect environmental factors. Two statistical techniques were employed to reveal these patterns - hierarchical cluster analysis and non-metric multidimensional scaling (MDS). The software program PRIMER v 4.0 beta was employed for these analyses.

Mean values of densities for each (15 mm) size class were calculated for each of the four sites. This was repeated for each month's data to explore whether any temporal effects were evident. Data were fourth-root transformed within PRIMER to downweight the effect of rare or exceedingly abundant frequencies (see Clarke and Warwick, 1994). The Bray-Curtis similarity index was employed for all analyses.

RESULTS

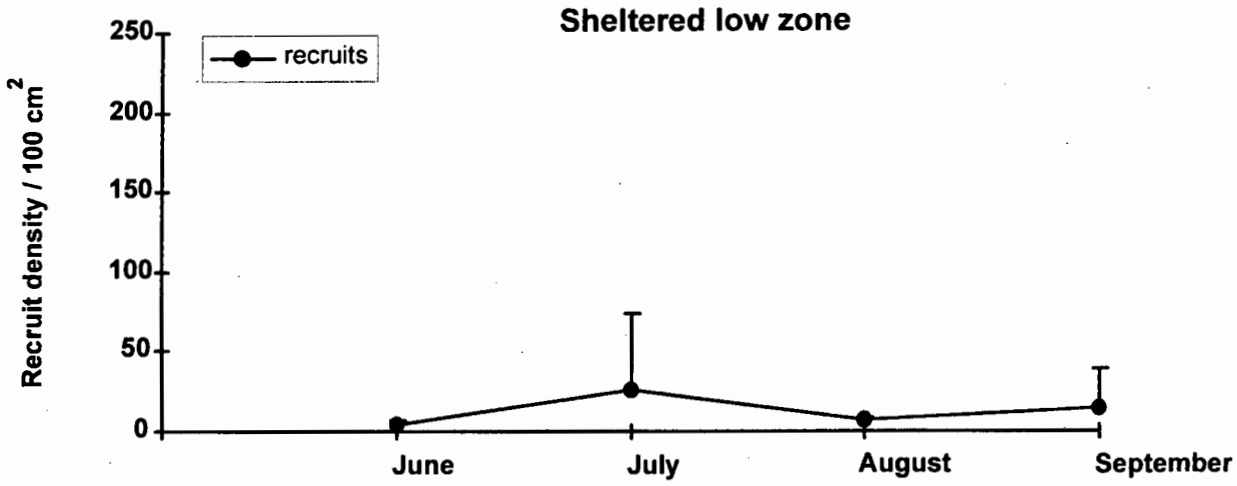
1 Natural recruitment

Natural recruitment fluctuated temporally and varied substantially between sites. This is best illustrated in Figure 2.1. The density of recruits was greatest at the exposed high shore site, averaging 136 per 100 cm^2 (see Table 2.1). The low shore in the wave exposed area had the next-highest density of recruits (81 per unit area). There was a two-fold difference between the exposed high location and the sheltered high site; this site exhibiting an average of 64 recruits per unit area. The low shore in the more sheltered area had a meager 13 recruits per unit area, resulting in a ten-fold difference between highest and lowest recruitment sites.

Table 2.1 Mean (+ S.D.) density (numbers/100 cm^2) of recruits for June to September replicates at exposed and sheltered sites. The average density for each site is given in bold.

	Sheltered zone		Exposed zone	
	Low shore	**High shore**	**Low shore**	**High shore**
June	4 (3)	60 (18)	96 (89)	163 (72)
July	27 (47)	54 (23)	104 (62)	120 (71)
August	7 (2)	69 (15)	68 (30)	145 (47)
September	14 (25)	71 (28)	55 (56)	114 (51)
Average	**13**	**64**	**81**	**136**

A three-way ANOVA on all replicates revealed that mussel recruitment to the exposed area in Camps Bay was significantly higher than recruitment to the sheltered area ($n = 96$, $\alpha = 0.05$, $p < 0.001$). The effect of height was also significant - the density of recruits in the high zone



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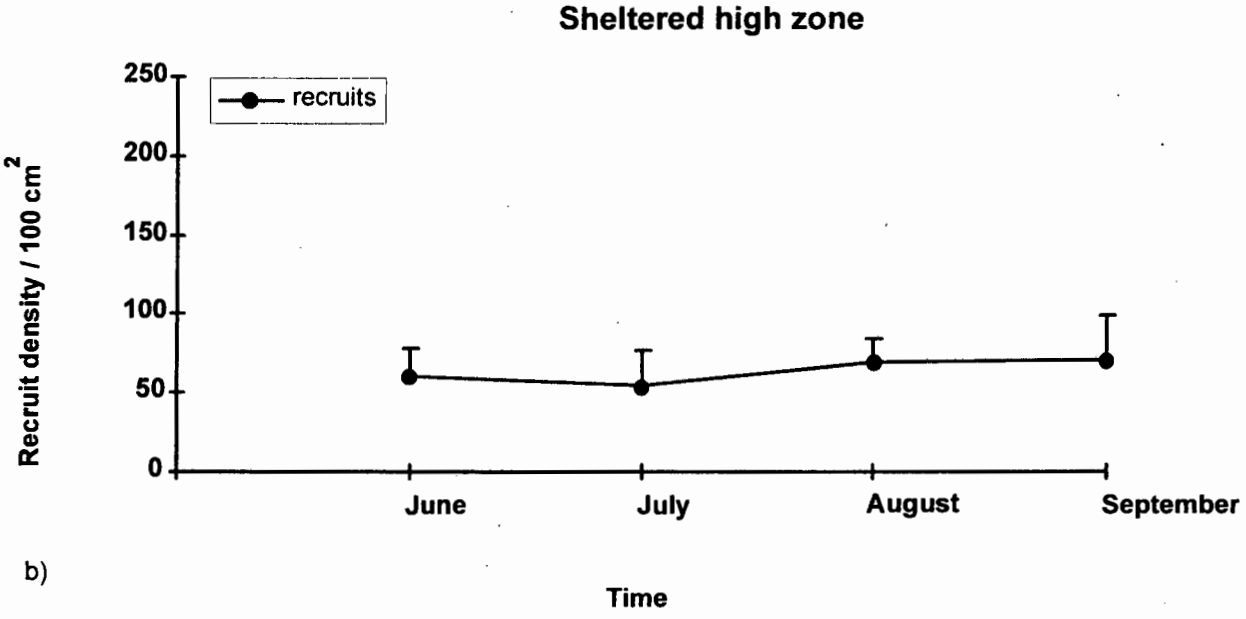

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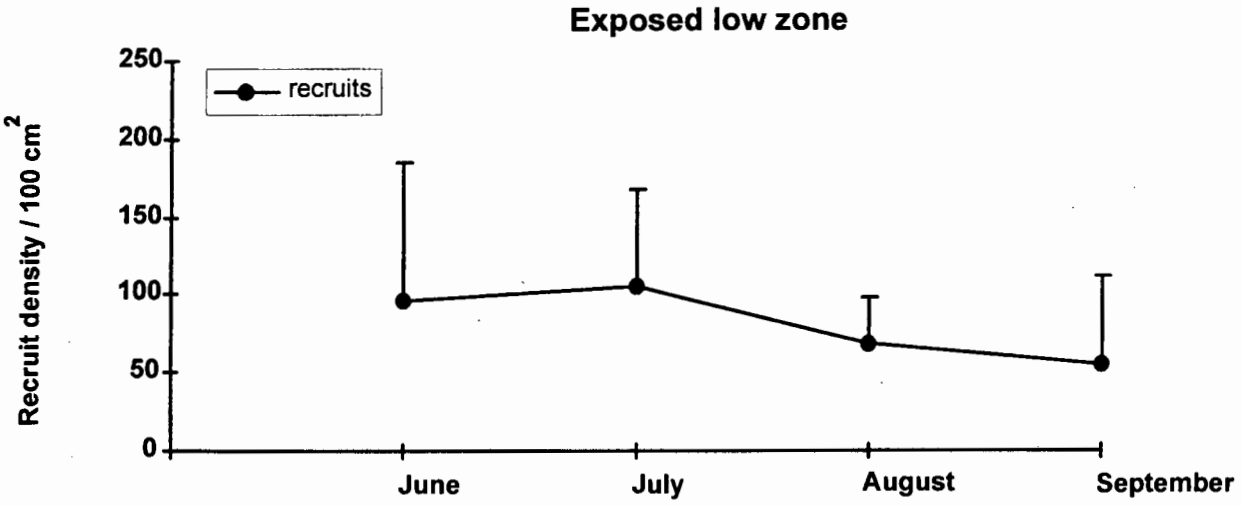

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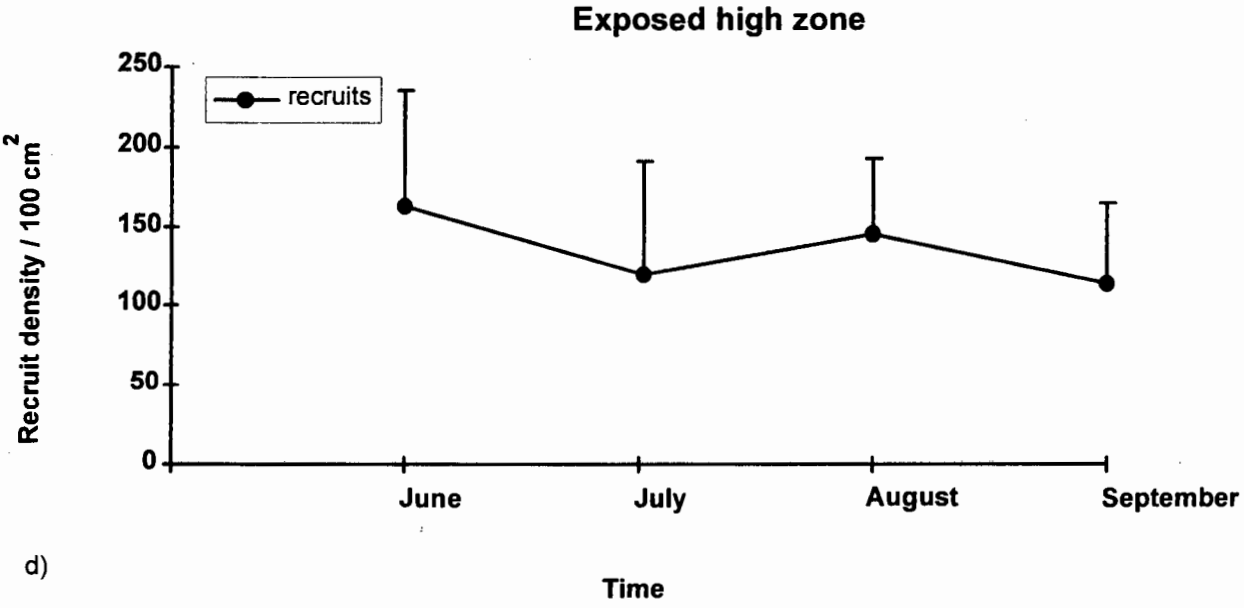


d)

Figure 2.1 Graphical representation of recruit densities (per 100 cm^2) recorded for June to September 1993. Sheltered and exposed areas were sampled at both high and low tidal elevations. Error bars depict standard deviations.

exceeding that in the low shore ($p < 0.001$). Most informative is that the temporal effect was insignificant - these patterns are (statistically) consistent from month to month ($p > 0.5$). No interactive effects were evident ($1 < p > 0.2$).

2 Recruitment to artificial substrate

Many of the scourers were removed by wave action as winter storms beset the west coast during the experimental period. Losses were recorded when sites were revisited and new scourers were set down to replace missing ones. Surprisingly enough, the sheltered high site experienced the highest loss (55%), but this may have been due to human interference since curious visitors were seen in this vicinity. The exposed high site lost 50% of its scourers, compared with a 47% loss at the exposed low site and only 14% in the sheltered low area. The exposed low site had the highest overall recruitment to the artificial substrate (15 individuals per scourer), followed by the exposed high site (11 scourer^{-1}), the sheltered low site (6 scourer^{-1}) and the sheltered high site (5 scourer^{-1}). The mean size of all recruits was 2.34 mm ($n = 519$). The maximum size of young mussels recruiting to the scourers was 9.89 mm, but 95% of the recruits were less than 5 mm in length. As no recruits were seen on the surrounding bare rock, it is probable that the recruits settled directly in the scourers and did not move there secondarily.

The statistical analysis performed on standardized data revealed that significantly more mussels recruited to scourers in the exposed area than to the sheltered area ($n = 52$, $\alpha = 0.05$, $p < 0.05$) but differences between low and high tidal elevations were insignificant ($p > 0.8$). The latter result is most interesting in view of the fact that natural recruit density was significantly greater at the higher elevation.

3 Recruit-adult relationship

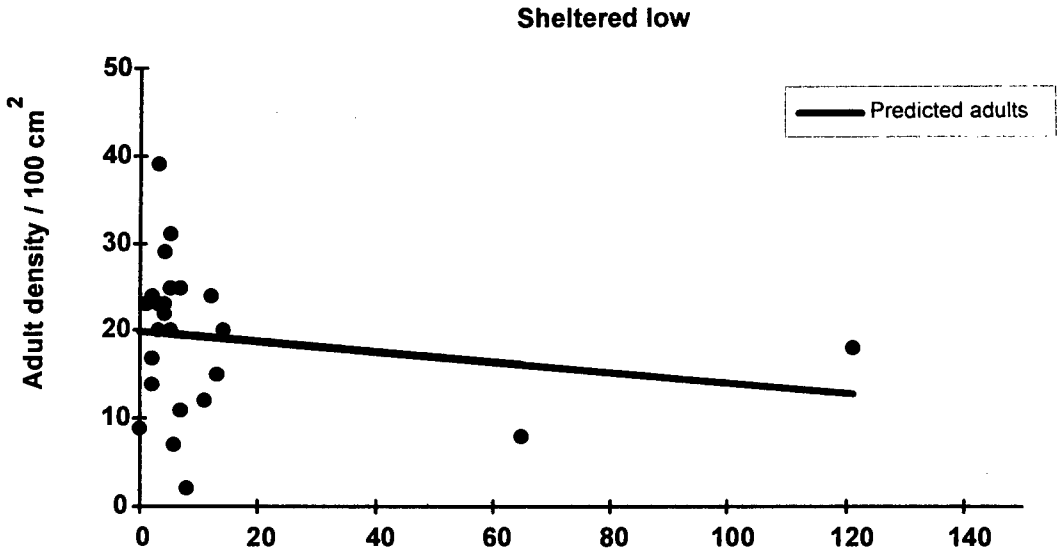
There was considerable temporal variability in the recruit-adult relationship in the mussel bed at all four sites. R-square values from linear regression analysis (presented in Table 2.2) indicate the high degree of temporal and spatial variation. Differences between sites were also evident. Generally speaking, the amount of variation in adult density explained by recruit density was extremely low for the exposed high site - none of the adult density was explained by recruit density during September and a maximum of 28% of the variability was recorded in July. The relationship for the sheltered low location was also low, ranging from 0% in July to 57% during September. A slightly stronger recruit-adult relationship was evident at the exposed low site. For the months of June and August, recruit density accounted for 20% of the adult density, increasing to 28% in July and 84% in September. The sheltered high area showed a consistently strong recruit-adult relationship with the exception of the month of

September (18%). In June, 52% of the variation in adult density was attributable to density of recruits. The relationship increased to 71% in July but dropped to 40% in August. The relationships were insignificant ($p > 0.05$ for each; actual p-values are recorded in Table 2.2), with the exposed low shore in September ($p < 0.01$, slope = 0.67, y-intercept = 28), the sheltered low shore in September ($p < 0.05$, slope = -0.3, y-intercept = 27) and the sheltered high shore in July ($p < 0.025$, slope = 0.97, y-intercept = 19).

Table 2.2 R^2 values (presented as percentages) for linear regressions of recruit versus adult densities performed for exposed and sheltered zones, high and low shores. Separate regressions were conducted for the months of June through to September 1993. An additional analysis was conducted on pooled data. Significance (S) or non-significance (NS) of the regression slopes are given with the respective p-values; significant statistics are highlighted and their slopes and y-intercepts are detailed in the text.

	Exposed zone				**Sheltered zone**			
	Low shore		**High shore**		**Low shore**		**High shore**	
	R^2	**Sig.**	**R^2**	**Sig.**	**R^2**	**Sig.**	**R^2**	**Sig.**
June	20 (n = 6)	NS (p > 0.1)	21 (n = 6)	NS (p > 0.1)	9 (n = 6)	NS (p > 0.25)	52 (n = 6)	NS (p > 0.05)
July	28 (n = 6)	NS (p > 0.1)	28 (n = 6)	NS (p > 0.1)	0 (n = 6)	NS (p > 0.25)	**71 (n = 6)**	**S (p < 0.025)**
August	20 (n = 6)	NS (p > 0.1)	4 (n = 6)	NS (p > 0.25)	13 (n = 6)	NS (p > 0.1)	40 (n = 6)	NS (p > 0.05)
Sept.	**84 (n = 6)**	**S (p < 0.01)**	0 (n = 6)	NS (p > 0.25)	**57 (n = 6)**	**S (p < 0.05)**	18 (n = 6)	NS (p > 0.1)
June - Sept.	3 (n = 24)	NS (p > 0.1)	3 (n = 24)	NS (p > 0.1)	3 (n = 24)	NS (p > 0.1)	**23 (n = 24)**	**S (p < 0.005)**

When the sites were examined for an overall adult-recruit relationship over the four month period, only a small proportion the variation in adult density was explained by recruit density. The line-fit plots (Figure 2.2) display the adult-recruit associations for each site. The exposed high and low sites have similarly low slopes that indicate a positive but non-significant relationship between recruit and adult densities ($p > 0.1$). Just 3% of the variation in adult density was determined by recruitment for both locations. Most unexpectedly, adult densities tend to decline with increasing recruit density at the sheltered low site, but again the density of recruits is a poor indicator of adult density (3% accountability, $p > 0.1$). The relationship is stronger at the sheltered high location (23%), and is highly significant ($p < 0.005$, slope = 0.22, y-intercept = 45).



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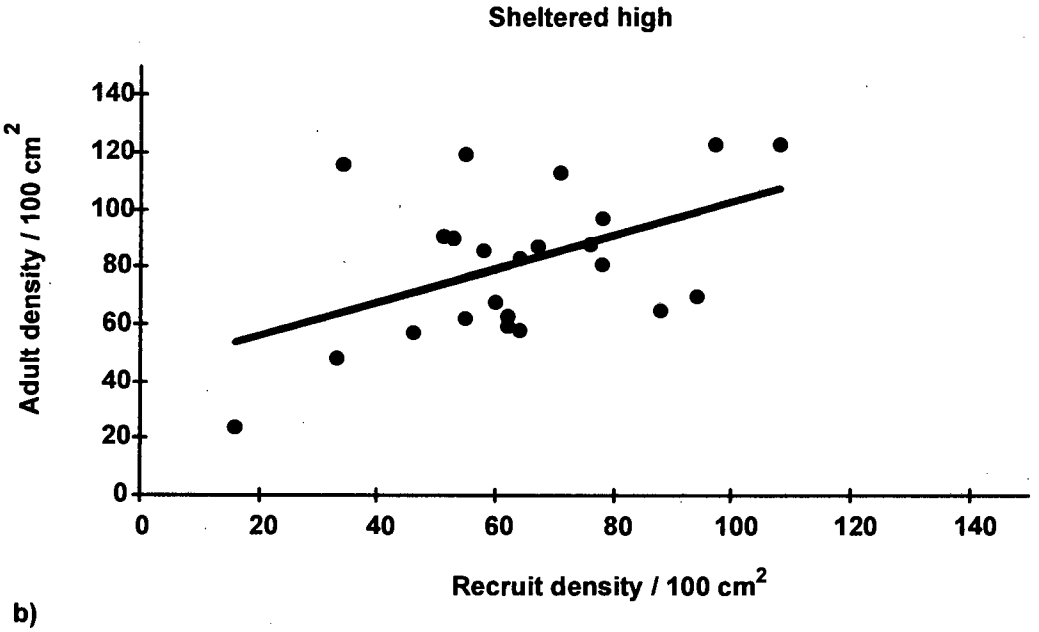

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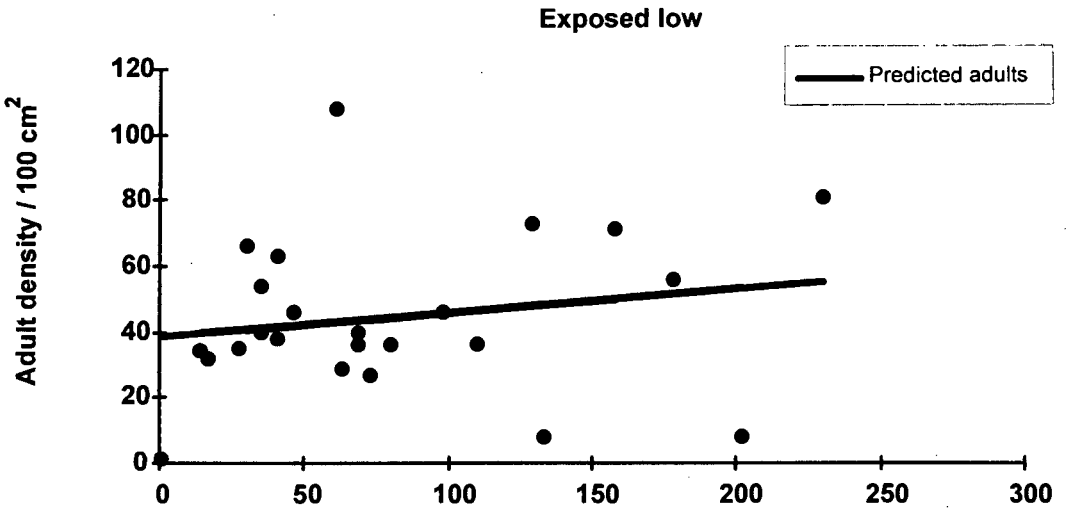

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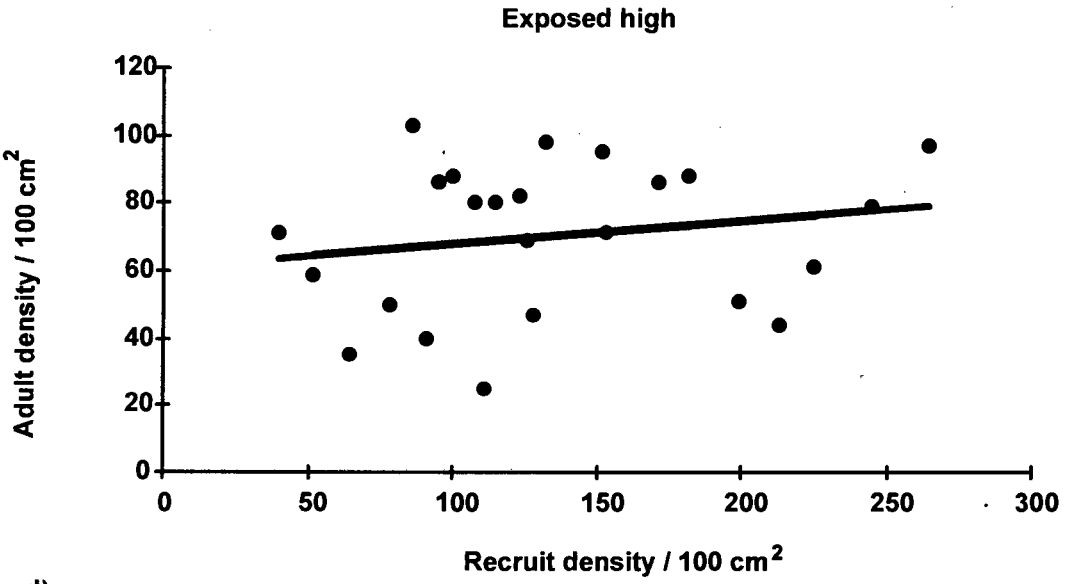

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Figure 2.2 Linear regressions of adult densities on recruit densities for sheltered and exposed areas. High and low zones are represented in each area. Data are pooled for June to September 1993. See text for details.

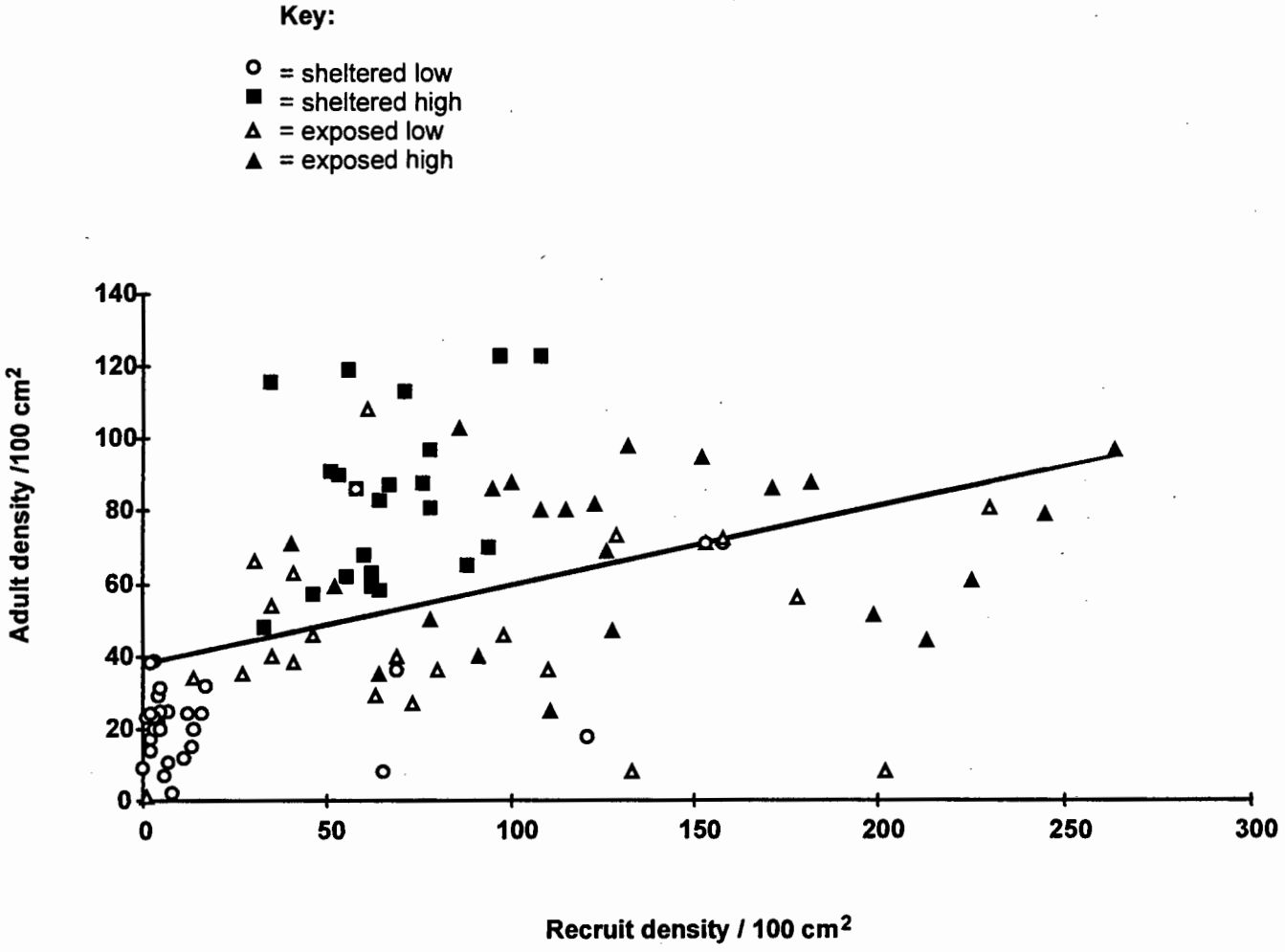


Figure 2.3 Density of adults vs. density of recruits in same quadrats for sheltered and exposed, high and low shore sites. Data were collected from June to September 1993. The key to symbols used is displayed above.

The Camps Bay study site as a whole exhibited a significant relationship between recruit densities and adult densities ($p < 0.0005$, slope = 0.22, y-intercept = 38, n = 96). The density of recruits explained 19% of the variation in adult density over the four month experimental period. Figure 2.3 illustrates the interesting phenomena of greater recruitment intensity and greater adult densities at higher tidal elevations for both sheltered and exposed areas. Adult densities are highest at the sheltered high site and recruitment densities peak at the exposed high site. The sheltered low site has conspicuously low densities of recruits and adults relative to the other sites (see Figure 2.3). Actual densities of recruits and adults collected over four months, from each site, is given in Table 2.3.

Table 2.3 Densities of recruits and adults (per 400 cm^2) in sheltered and exposed areas, low and high shores. Values are total densities collected during the experimental period from June to September 1993.

Exposed zone				Sheltered zone			
Low shore		High shore		Low shore		High shore	
Recruits	Adults	Recruits	Adults	Recruits	Adults	Recruits	Adults
1940	1064	3253	1685	307	461	1528	1947

4 Population patterns

The dendrogram (Figure 2.4) illustrates very perceptible patterns from results of the hierarchical cluster analysis. Perhaps most striking is that there is no temporal separation of any of the sites: that is, any particular site is most similar to itself in size-frequency attributes for each month sampled. Comparisons between sites is equally enlightening. The sheltered low site (for June to September) is approximately 78% similar in size-frequency composition to the exposed low site. The next grouping, between sheltered high and exposed high localities is even more firm, exhibiting approximately 86% similarity.

Non-metric MDS was then used to map the similarity matrix in two dimensions (Figure 2.5). The Euclidean distance between points on the map delineates the degree of similarity between sites (and/or samples). Conforming with the output from the cluster analysis, monthly samples of individual sites are seen clumped together, indicating the lack of temporal effects. What becomes apparent in the MDS map is that the sheltered low site is segregated from the remaining sites (at all times), indicating its dissimilarity in population composition. The exposed high and sheltered high sites are concentrated together, depicting their close similarities. Both remain separated from the exposed low area. The stress coefficient is exceptionally low (0.02),

Dendrogram of Camps Bay length-frequency data

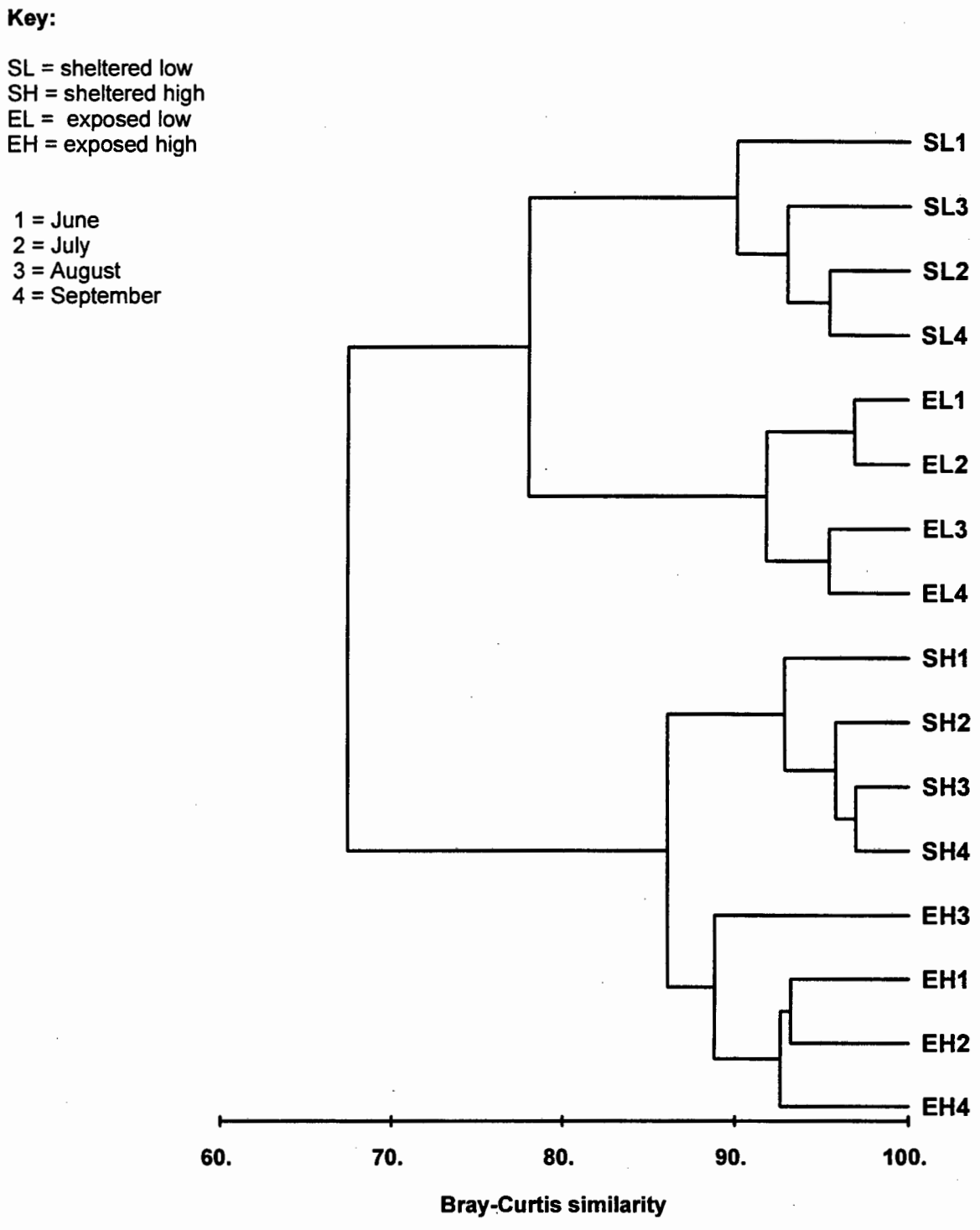


Figure 2.4 Dendrogram for hierarchical clustering of sheltered and exposed, high shore and low shore sites, for four months, based on Bray-Curtis similarities. The key for sites and months is given in the left-hand corner.

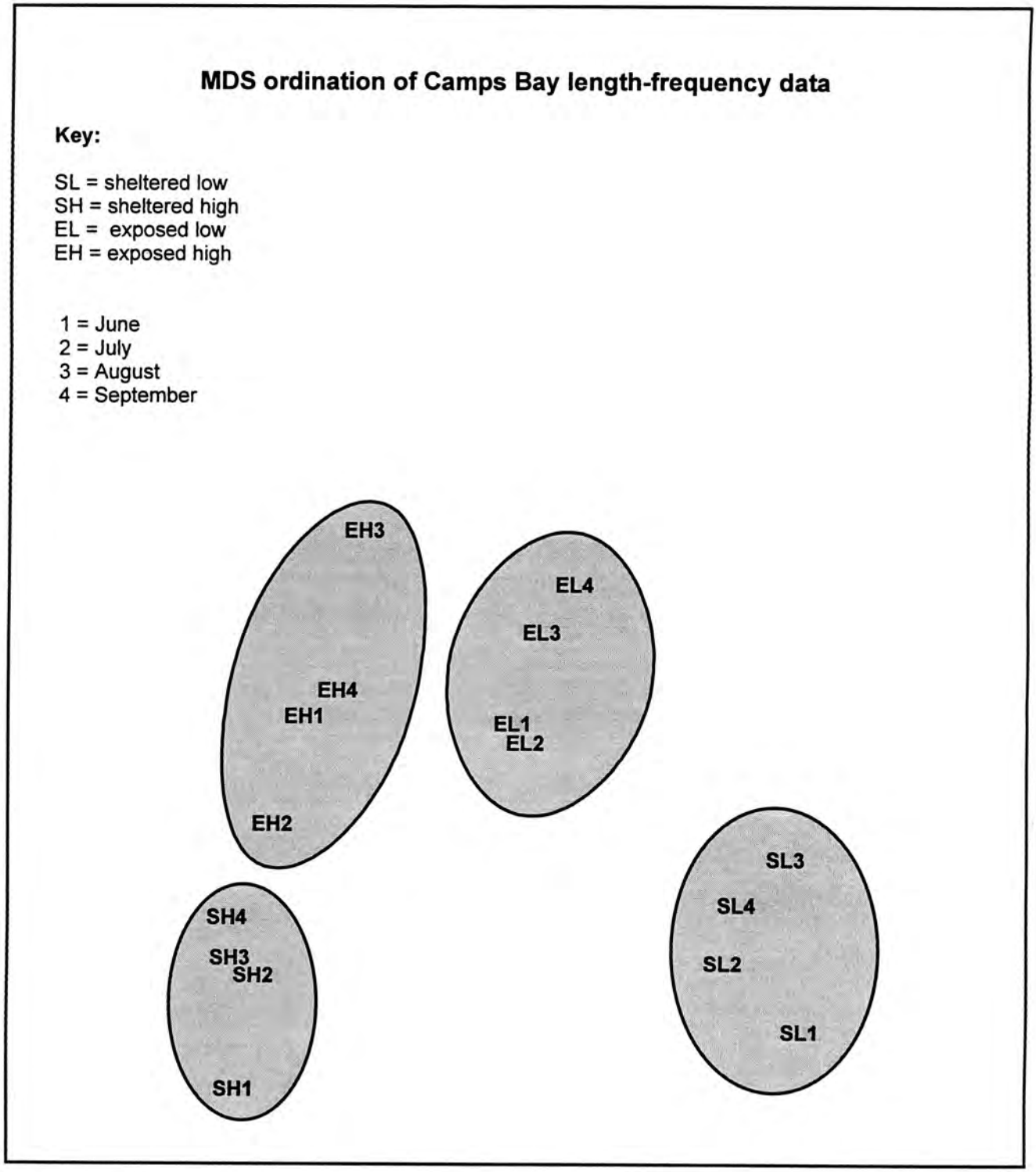


Figure 2.5 MDS ordination of sheltered and exposed sites at Camps Bay for June through to September 1993 based on Bray-Curtis similarities (stress = 0.02). The key for the various sites and times is given in the left-hand corner of the map.

indicating that the low dimensional configuration is an excellent representation of the multidimensional structure inherent in the similarity matrix (Clarke and Warwick, 1994).

DISCUSSION

The importance of recruitment in regulating community structure is strongly emphasized in the literature, but its precise role is not well understood (Fairweather, 1991; Fogarty *et al.*, 1991; Grosberg and Levitan, 1992). The contribution of such biotic processes is likely to vary with diverging environmental factors. Moreover, recruitment can be episodic (stochastic) and its relationship to adult densities will often exhibit temporal variation. This study relates recruitment patterns of *Mytilus galloprovincialis* at Camps Bay to their environment (wave exposure and tidal height) and explores the relationship between recruitment and adult density under different sets of these environmental conditions. Population demography is then used to graphically examine differences in mussel community structure between sites on the shore, which may reflect differences in environmental conditions.

Exposed shores are submerged for longer periods than are protected shores and (by definition) experience heavier wave action. As such, one would predict an increased supply of larvae to these areas, resulting in higher recruitment rates. In accordance with expectations, both "natural" mussel recruitment and recruitment to artificial collectors in the wave-exposed site at Camps Bay was significantly higher than in the more protected area ($p < 0.05$ and $p < 0.001$ respectively). The trend mimics the results of "natural" recruitment recorded for Camps Bay in chapter one and in this study the pattern was temporally consistent for the months of June to September 1993 (in the natural population). By comparison, Petraitis (1991) found no consistent differences in recruitment of the mussel *M. edulis* between sheltered and exposed shores in Maine, although recruitment was generally higher on wave-swept shores (Petraitis, 1991). Menge (1991) revealed a more complex pattern of recruitment of the barnacle, *Semibalanus balanoides* in New England, the relationship between recruitment and wave exposure varying with tidal height. Barnacle recruitment in the high intertidal zone changed little with wave action but in the mid and low zones, recruitment density decreased with a reduction in wave action. Other studies have shown increased settlement of invertebrates on wave-exposed shores (Seed, 1969 in his study on *M. edulis* along the Yorkshire coast; Bertness et al, 1992 for *S. balanoides* at Rhode Island) but their subsequent recruitment was not investigated.

It is highly conspicuous that recruitment of *M. galloprovincialis* to the natural mussel beds at the Camps Bay study site was significantly greater in the high intertidal zone ($p < 0.001$). The lack of temporal variation in the trend for the months observed is equally noteworthy. Connell (1972, 1975) discusses how the upper limits of distribution of intertidal animals are set by

physical factors, desiccation and heat stress by insolation leading to differential mortality in high zones. This appears to be the case for *M. edulis* on the Yorkshire coast, when plantigrades settling in the mid-high shores exhibited elevated mortality due to desiccation (Seed, 1969). Increased post-settlement mortality of *Chthamalus anisopoma* in the upper limits of its distribution was attributed to the increased thermal capacity of basalt rock compared with granite (Raimondi, 1988). Underwood and Denley (1984) proposed that several alternative mechanisms may operate to limit both upper and lower distribution, with emphasis placed on the role of larval supply. In a previous study, Denley and Underwood (1979) found that both upper and lower limits of *Tesseropora rosea* and *Tetraclitella purpurescens* were determined primarily by the settlement of cyprid larvae. It was not obvious whether the lack of spat at the highest shore levels was due to decreased submersion or preference for lower sites. Since the publication of these papers, more attention has been focused on the effect of tidal elevation on settlement and recruitment in recent literature. Settlement of the acorn barnacle, *S. balanoides* decreased with increasing tidal height (Bertness *et al.*, 1992). Recruitment of a variety of invertebrate species recruited in greater abundance to artificial panels situated in the lower intertidal zone than to the upper zone in N.E. Scotland (Turner and Todd, 1993). The results of the present study on the natural mussel beds are in accordance with patterns described in chapter one of this thesis. Recruitment is greater high on the shore than low on the shore, and adult densities follow this pattern (see Chapter one). Whether these trends are attributable to differences in larval supply and settlement or to differential post-settlement mortality was not determinable from the data, but the ability of *Mytilus* to resist desiccation (Griffiths *et al.*, 1992; Hockey and van Erkom Schurink, 1992) seems to be reflected in the high numbers of recruits located at the higher tidal elevation.

Results from the artificial recruit collectors suggest that mortality may be the cause of differential recruit abundance between sites in the Camps Bay population. Recruitment to scourers placed in the high and low zones was statistically equivalent over the four month period although more recruits were collected from the low shores. Since these scourers were replaced monthly, only small recruits were collected (< 10 mm in length, average size = 2.34 mm), which suggests that greater mortality rates of older recruits in the lower zones may be responsible for the patterns observed in the natural population. The specific cause of such mortality is unknown, but the predatory gastropod *Nucella cingulata* and heavier wave action at these are possible agents that need to be investigated in future research.

Recruitment of *M. galloprovincialis* was generally a poor indicator of adult abundance at Camps Bay on a month-to-month basis, although this varied spatially and temporally. Between-site comparisons for the full experimental period revealed that no recruit-adult

relationship existed at either the exposed (high and low shore) sites, or at the sheltered low shore site ($p > 0.1$). It was, however, significant at the sheltered high shore site ($p < 0.005$) where 23% of the variability in adult densities was explained by recruit densities. An averaging-out effect (see Risser *et al.*, 1984) of the smaller, between-site scale appears to take place at the larger scale of the entire Camps Bay study site - overall, the recruit-adult relationship is significant ($p < 0.005$) although only 19% of adult abundance is attributable to recruitment. The temporal and spatial variability in the recruit-adult density relationship should not be surprising, considering the stochastic nature of recruitment itself and this has been reported elsewhere. Menge (1991), in his investigation of intertidal community structure in New England and Panama, found the relative role of recruitment to vary between localities and species. Recruitment of the barnacle *S. balanoides* in New England explained 36% of the variance in adult abundance. In Panama, recruitment of several species of solitary sessile bivalves and barnacles explained from 55 to 97% of the variation in adult density, but recruit density was a poor indicator of adult density for the barnacle, *Chthamalus fissus* (29%). Davis (1988) illustrated temporal variability in the recruit-adult relationship of the ascidian, *Podoclavella moluccensis* from one year to the next. In the first year, recruit density predicted 70% of the variation in adult density but this declined to 20% in the second year. A review of the importance of recruitment density on adult density by Menge and Farrell (1989) indicated that there is no consistent relationship between the two. These results clearly indicate the need to address other causes of variation on adult abundance and community (population) patterns in general (see Menge and Farrell, 1989; Petraitis, 1991). In the following chapters, mortality rates and disturbance are investigated to establish the influence these factors have on mussel population patterns.

Other sources of recruitment variability that were not addressed in this study are the presence or absence of grazers, predators and conspecifics, space availability, surface contour or substrate suitability: Menge (1991) observed enhanced recruitment of the barnacle, *Chthamalus fissus* at high shore levels in Panama. Recruitment in this zone was greatest in the presence of grazing molluscs and in the absence of predaceous gastropods. This relationship between recruitment and predators was repeated in the low zone. However, in the mid zone, recruitment was highest in the absence of grazing molluscs. Petraitis (1990) reported that recruitment of *M. edulis* is depressed by the grazer *Littorina littorea*, but was insignificantly affected by the predatory gastropod, *Nucella lapillus*. Space availability was seen to influence settlement of *S. balanoides* in Rhode Island (Bertness *et al.*, 1992). The authors indicate that settlement seems targeted at low tidal heights provided there is space available. When space becomes limited, settlement shifts to tidal heights where space is available. The influence of surface contour on settlement patterns has also been investigated (Wethey, 1984; Raimondi, 1988). Settlement of *Balanus balanoides* was higher in cracks than

on smooth surfaces in New England (Wethey, 1984). Likewise, *Chthamalus anisopoma* settles in higher numbers when surface rugosity increases in the Gulf of California (Raimondi, 1988). A similar relationship was established for *M. edulis* recruitment in Maine (Petraitis, 1990). Larvae or recruits often show a preference for certain substrate types. Young (1991) illustrated the nonrandom recruitment of the barnacle, *Chthamalus fragilis* onto the axils of the cordgrass *Spartina alterniflora*, although survival here was not higher than on any other position of the plant. Barnacles enhance the settlement and recruitment of *M. edulis* (Seed, 1969, Petraitis, 1990). Recruitment of the intertidal barnacle, *Tetraclita panamensis* occurs mainly on the shells of conspecific adults (Sutherland, 1987). *Tesseropora rosea*, on the other hand, rarely settles on adult shells (Denley and Underwood, 1979). Byssus threads, filamentous algae and hydroids were identified as suitable substrates for the settlement of *M. edulis* (Bayne, 1964; Seed, 1969). Primary settlement of *M. galloprovincialis* onto filamentous substrates (rope) followed by secondary settlement to adults was observed in Ria de Vigo, N.W. Spain (Caceres-Martinez *et al.*, 1993).

A final comment on the use of artificial recruit collectors such as the dish scourers used in this study addresses the issue of alternative causes of recruitment variability. While the scourers control for the effects of substrate type, uniformity and space availability, they are not selective in their accumulation of algae, sand or organisms such as isopods. By now it should be clear that these variables may affect recruitment patterns, to an extent that remains undetermined. The factors described in the previous paragraph all operate at a relatively fine scale and their overall contribution to recruitment or population patterns is not known. Their inclusion in models of community dynamics may, nevertheless, enhance the predictiveness of such models.

Population patterns can be illustrated in a relational fashion such that similarities (dissimilarities) between populations emerge. These patterns are believed to depict past or present environmental conditions (Clarke and Warwick, 1994). Hierarchical cluster analysis grouped the low zones of the sheltered exposed areas on the basis of length-frequency data. These sites exhibited remarkable likeness, with a similarity score of 78%. The sheltered high site and exposed high sites were demographically even more similar, being grouped at 86% on the Bray-Curtis similarity scale. Of note was the lack of any temporal effect, each site being most similar to itself for any month from June to September. This was also valid in the non-metric MDS analysis. The MDS illustrated additional information in that the sheltered low site was least similar to any of the others in size-frequency composition. Whether wave exposure and tidal elevation act in combination to produce these population patterns may not be inferred from the results - causal mechanisms are not illustrated by the analysis, but the similarities or dissimilarities between sites are conspicuous. Community patterns and

processes at these sites are explored further in the following chapters, with emphasis on their correlations with wave exposure and shore height.

CHAPTER 3

Are differences in growth and mortality related to wave action and/or height on the shore?

INTRODUCTION

One of the most obvious patterns on the rocky shore is that animals often show differences in size distributions depending on where they inhabit the shore. These differences in size are indicative of the prevailing environmental conditions that influence the growth rates and/or survival of organisms. Previous work has on mytilids has certainly shown this to be the case. Some of the factors influencing growth include density, frequency of submergence, temperature and silt levels, to name but a few (Du Plessis, 1977; Griffiths, 1981; Barkai and Branch, 1989; van Erkom Schurink and Griffiths, 1990; van Erkom Schurink and Griffiths, 1993) . Du Plessis (1977) found the indigenous black mussel *Choromytilus meridionalis* showed considerable variation in growth within his study area in Saldanha Bay. Slower growth rates were attributed partly to overcrowding but the relationship between density of animals and growth is not always a simple one. In a study on four South African mussel species (*C. meridionalis, Perna perna, Aulacomya ater and Mytilus galloprovincialis*), it was discovered that at low densities, crowding positively affects growth whereas at high densities all species' growth is retarded (van Erkom Schurink and Griffiths, 1993). Barkai and Branch (1989) found that experimentally caged *C. meridionalis* grew more slowly than did uncaged mussels, presumably due to smothering by other animals. Interestingly though, the reverse effects were true for *Aulacomya ater*. The influence of temperature on growth may also be species-specific: while the growth rates of *M. galloprovincialis* and *Perna perna* are accelerated at higher temperatures, cold water species such as *A. ater* and *C. meridionalis* show retarded growth in warmer waters (van Erkom Schurink and Griffiths, 1993). Clearly, food availability will determine growth rates of animals and for sessile animals this is especially pertinent since food levels fluctuate unpredictably over a wide range (see Griffiths and King, 1979). Growth rates will not be stable over the entire year in temperate regions and indeed Crawford and Bower (1983) found growth in *P. perna* to vary seasonally.

Hydrodynamic forces also play a major role in determining the growth of organisms. The effect of wave action on growth has been observed in *P. perna*. Apparently the physical action of swell and surf breaks down food and makes it readily available to filter-feeders and Perna grows faster in areas of higher wave energy (Berry, 1978). An investigation of the growth performance of four mytilids (van Erkom Schurink and Griffiths, 1993) revealed that all four species grow faster at higher water circulation rates. Animals residing within even a relatively small area such as the Camps Bay study site will be exposed to a range of hydrodynamic conditions which might be related to topography (e.g. channels as opposed to bays) or height on the shore. There are visible differences in sizes exhibited by *M. galloprovincialis* at the Camps Bay study site that appear to be linked to physical wave energy and/or tidal height. First, animals that are found further from the mean low water mark tend to achieve smaller maximum sizes than those found closer to low tide levels (see also Chapter

one). This may be because animals higher up on the shore are usually not inundated with water during low tides and so have less feeding time than those lower down. Filter-feeding animals found in wave-exposed areas may also benefit from a more regular food supply (by virtue of heavier wave action) which animals in sheltered areas do not experience. Secondly, animals that are regularly exposed to the sun are vulnerable to desiccation and thus have imposed upon them a physiological stress that animals lower down do not experience (at least not to the same degree). Animals that are physiologically stressed will more than likely grow more slowly than animals not encountering prolonged aerial and heat exposure.

Surprisingly enough, *M. galloprovincialis* is a comparatively poorly explored mussel and not much is known of its ecology in natural populations (Ceccherelli and Rossi, 1984). *M. galloprovincialis* has only fairly recently invaded the South African coastline (Griffiths *et al.*, 1992) and although it's growth performance on mariculture ropes and steel frames has been recorded along with that of the three common indigenous mytilids (van Erkom Schurink and Griffiths, 1993) no growth data have been recorded for it when it is growing on the shore in South Africa. Since cultured mussels (often grown on suspended ropes) have a different ecology to animals inhabiting the rocky shore, they are likely to exhibit different growth rates. The objective of this study was to obtain *in situ* measurements of both growth and mortality and to determine their relationship with wave action and position on the shore.

Because the primary objective was to determine if growth and mortality are related to wave action and zonation, the observations were confined to a period of four months over the winter season when storm effects are at their greatest. This temporal restriction means that the data cannot be extrapolated to annual patterns.

MATERIALS AND METHODS

Three sets of data were collected to measure growth and mortality and all collections were made during Spring low tides:

1. Tagged adults

Because mussels are tightly packed on the shore (particularly in the wave-exposed zone) it was necessary to clear areas of mussel bed so that animals could be properly marked and labelled: 30 x 30 cm plots were cleared in the sheltered and exposed areas and on the low and high shore zones in each area. Six replicate areas were cleared for both high and low shores in each area. During the period 2nd - 5th July 1993, 10 adults on the edge of each cleared area were marked with Pratley putty and a number was engraved in the putty so that the growth of each adult could be followed. There were in total 60 marked adults for the

exposed low shore and 60 for the high shore, and the same for the sheltered zone. Animals were measured *in situ* to the nearest 0.1 mm with vernier calipers. At the next set of spring tides it was noted that 60% of the labelled animals at the exposed low site were missing - they had either been dislodged as a result of strong storms that were prevalent during those two weeks, or the labels had been washed off. As a result, another 60 adults were labelled and measured at this site. After four months, labelled adults were removed and were remeasured. These labelled animals were also to be used to establish relative rates of mortality at the various sites.

To distinguish the loss of adults from the loss of labels, a control was set up at each site during 2nd - 5th July. For each position on the, 20 mussels (or 10 for the exposed low shore) were glued to the rock with Z-spar putty and each animal was tagged with Pratley putty in the same manner as for the growth plots. Survival of tags on these animals was monitored for four months. As no tag lass was recorded over this period, it can safely be assumed that losses recorded in the experimental plots are indicative of mortality, and do not simply reflect tags being detached or eroded away.

An analysis of covariance was performed with the SYSTAT v 5.0 statistical software package to determine whether growth differed between the four treatments (sheltered high, sheltered low, exposed high and low sites). Regression slopes were tested for homogeneity prior to the testing of treatment effects. A one-way ANOVA tested for the significance of differential mortality rates between sites.

2. Recruits

Plots that had been set up for adult growth were intended to be used to measure the growth of young mussels which were expected to recruit to the (30 x 30 cm) cleared areas. Unfortunately, few if any mussels recruited to these plots over the first two months. In August 1993, however, carpets of recently settled mussels were found attached to barnacle beds in the exposed area and to rocks or amongst algae in the sheltered zone. These cohorts appeared to be of equal age at the two sites and were therefore targeted for monitoring growth in young mussels. Both of these recruitment sites were situated near L.W.S. On the 18th August five 10 x 10 cm areas were cleared of recruits from both sheltered and exposed zones to determine their size composition. The sites of recruitment were sampled again two months later, in the same manner.

Mussels were separated from each other and from barnacles/algae and were then counted, measured and analyzed with a Joyce-Loebl (micro-magiscan 3) image analyzer and JLGenias software package (see chapter one for details).

3. Cohort analysis for the full size range of mussels

Cohort analysis encompasses various graphical and mathematical techniques that enable the growth rate of a population to be estimated from length-frequency data. The various techniques make certain assumptions about the data and about the biology of the organism in question so that growth curves may be fitted to the data. Two methods were used on the data to attempt to get the most accurate results: modal progression analysis (MPA) by a) Bhattacharya's (1967) method and FiSAT and b) the MULTIFAN method (Fournier *et al.* , 1990)[1]. The first MPA was performed mainly as a preliminary technique, as suggested by M. Kerstan (pers. comm.), but was found to be deficient and discarded. Because the limitations attending the Bhattacharya/FiSAT method are often not appreciated and the method inappropriately applied, a brief outline is given below of the reasons why it could not be applied in the present case.

Data collection for both these analyses began during the set of spring tides in the third week of June 1993. Samples were taken monthly for a four month period, terminating in the first week of October 1993. Mussels were removed from the sheltered and exposed zones and both high and low shores were represented in each zone. As with the previous experiment, six replicates were taken at each site on the shore and a 10 x 10 cm area of mussel bed was removed per location. Each of the six locations had been permanently marked by drilling a hole in the granite and hammering a nail, tagged with a cable tie, into the rock. The permanent marking of plots ensured that each 10 x 10 cm area would be removed next to or near the previous collections.

All mussels in this data collection were first frozen and subsequently measured using the Joyce-Loebl (micro-magiscan 3) image analyzer and JLGenias software package.

3.1 Modal progression analysis by Bhattacharya/FiSAT

As a test case, the software program FiSAT was used to perform MPA on data from the exposed zone consisting of the entire size range of mussels. This procedure infers growth

[1]The program is licensed to S.F.R.I. and all analyses were performed on the premises.

from the shift of modes (representing cohorts) over time (Gayanilo *et al.*, 1994). Distinct cohorts are identified from a size-frequency distribution and the mean of each cohort is established for each monthly sample. The means of successive cohorts are then subjectively linked so that a von Bertalanffy growth function (VBGF) may be fitted. For the first stage, Bhattacharya's (1967) method was performed on the (length-frequency) data which were resolved into modes, each representing a cohort (see Bhattacharya 1967; Castro and Erzini, 1988). This operation is performed by FiSAT. The method is sensitive to the size of the class frequency chosen successful (see Gayanilo *et al.*, 1994) and was run at constant size classes of a) 5 mm and b) 2 mm.

Visually, the fits obtained for 5 mm size classes were poor and chi-square tests revealed that the observed distributions were significantly different (at $p < 0.05$) from the expected distributions. Moreover, the employment of 5 mm size classes yielded less than the recommended 10 degrees of freedom (Gayanilo *et al.*, 1994). All subsequent calculations were therefore based on 2 mm size classes.

The size frequency distributions for 2 mm size classes produced distinct modes, from which it was possible to define cohorts. Even so, the results of the chi-square tests for each month indicated that the expected and observed distributions were significantly different ($p < 0.05$).

The plot of the means of the cohorts against time can theoretically be used by FiSAT to derive a VBGF. However, an additional problem arose when the programme was run: although not clearly defined as a limitation, the programme cannot derive growth functions if the data span less than 12 months because its plot spans a 2-year time period.

3.2 The MULTIFAN method

The method adopted by Fournier and Sibert (1990) in the software program MULTIFAN combines linear regression with techniques from robust statistical estimation theory and is flexible to large deviations from the model's hypotheses. This is necessary because the growth of some animals does not always strictly follow a VBGF (see e.g. Griffiths and King, 1979) and cohorts are not always best described with a normal distribution. There might be, for example, animals that are much longer than others of the same age and this may have an unjustified influence on the parameter estimates (Fournier *et al.*,1990). Another confounding factor is that it is common for cohorts to merge during development (Seed, 1969). However, the advantage of the MULTIFAN method is that it is less subjective than many other techniques (Fournier *et al.*, 1990; Fournier *et al.*, 1991; Terceiro *et al.*, 1992). Methodologies such as those employed by Cassie (1954), Macdonald and Pitcher (1979), Brey and Pauly (1986) and Sparre *et al.* (1989) rely on one or more stages of subjective decision-making and

it is possible for different users to make entirely different choices, resulting in estimations of the growth parameters that are dubious. MULTIFAN offers a graphical interface which allows the user to estimate and restrict the initial parameters so that the final parameters (number of age classes, von Bertalanffy K, L-infinity) may be computed more precisely. The program determines which parameters best describe the data by choosing fits with the highest log-likelihood values (Fournier *et al.* 1990).

Separate analyses were performed on data from exposed low and high shores and similarly for the sheltered high and low shores. All data were transformed to length-frequencies with a size class of 2 mm. Hypothesis tests were performed on the systematic searches (Fournier *et al.*, 1990) to establish the significance of the fits to the model. This hypothesis testing requires that a chi-square test be performed a) at the 90% confidence level to determine the number of age-classes of a distribution and b) at the 95% confidence level to determine whether length-dependent standard deviations should be incorporated into the model.

When standard deviations were allowed to vary, they either failed to produce a significantly better model or they estimated unacceptably high L-infinities. These models were therefore rejected. These results may be biologically or environmentally meaningful or may simply indicate that the assumptions of the model are not adequately met. Their relevance was not investigated in this study.

RESULTS

1. Tagged adults

1.1 Mortality

There loss of animals following the severe winter storms was significant, and varied according to zone and site (see Table 3.1). Not surprisingly, the exposed lower shore experienced the highest loss - 92% of the tagged animals were washed away, leaving only 5 out of the original 60 mussels. By comparison only 32% of the 60 labelled mussels were dislodged in the exposed high shore. The sheltered zone exhibited a considerably lower mortality rate than the exposed zone. The loss of adults also again higher for the low shore (47% loss) than the high shore (20% loss). An ANOVA performed on the data (6 replicates per site) revealed that mortality rates are significantly different between the four sites ($p < 0.01$). Tukey's post hoc comparisons test indicated that the exposed lower site experienced a significantly higher mortality rate than any of the 3 other sites ($p < 0.01$). Mortality in the sheltered low area was significantly different from the sheltered high area ($p < 0.05$), and no other comparisons were significantly different ($p > 0.1$). It is obvious from these results that mortality rates differ within

short distances at Camps Bay and specifically that losses in the low shore of each zone were consistently higher than for the high shore. Since the effect of height on the shore may be confounded with wave exposure when no environmental measurements are taken, the respective effects of wave energy and shore height are difficult to establish. However, logic dictates that the effects of shore height *per se* will yield higher mortalities in the high shore, so the fact that mortality was greater in the low shore suggests wave action was primarily responsible.

Table 3.1 The total number of tagged animals missing from each site after four months. These are also expressed as the percentage mortality for each site. The average growth (in millimeters) achieved by the remaining mussels is given as the growth increment for the four month experimental period. Values in brackets are standard deviations.

	Sheltered zone		**Exposed zone**	
	Low shore	**High shore**	**Low shore**	**High shore**
Nos. lost	28	12	55	19
Mortality (%)	47	29	91.6	32
Growth inc.	2.45 (2.8) n = 32	1.32 (1.8) n = 48	3.28 (2.2) n = 5	4.43 (2.6) n = 41

1.2 Growth

Variations in growth of labelled animals with respect to wave exposure and shore height are apparent from the differences in average lengths calculated from the June and October data. The increases in average size of the mussels represent the growth increments for each site over four months. These are given in Table 3.1, from which it can be seen that animals in the exposed zone grew faster than those in the sheltered zone. Mussels in the wave-exposed area and situated on the low shore grew 3.28 mm (on average) over four months while those higher up grew 4.43 mm over the same period. The growth increments for low and high shore mussels in the sheltered zone were 2.45 mm and 1.32 mm respectively.

Initial and final lengths from each site (of both zones) were used to perform an ANOVA. The regression slopes were found to be homogeneous and the analysis revealed a statistically significant difference in growth for the four treatments (sites) ($p < 0.01$). Tukey's post hoc test was performed to determine which site/s contributed to the statistical difference. The multiple comparisons test revealed that growth of animals at the sheltered high site was significantly slower than growth at any of the remaining three sites ($p < 0.03$). None of the other sites were different from one another ($p > 0.9$). These results should of course be viewed with caution because of a) the differences in sample size between the treatments and b) the sometimes very small sample sizes resulting from losses of labelled animals.

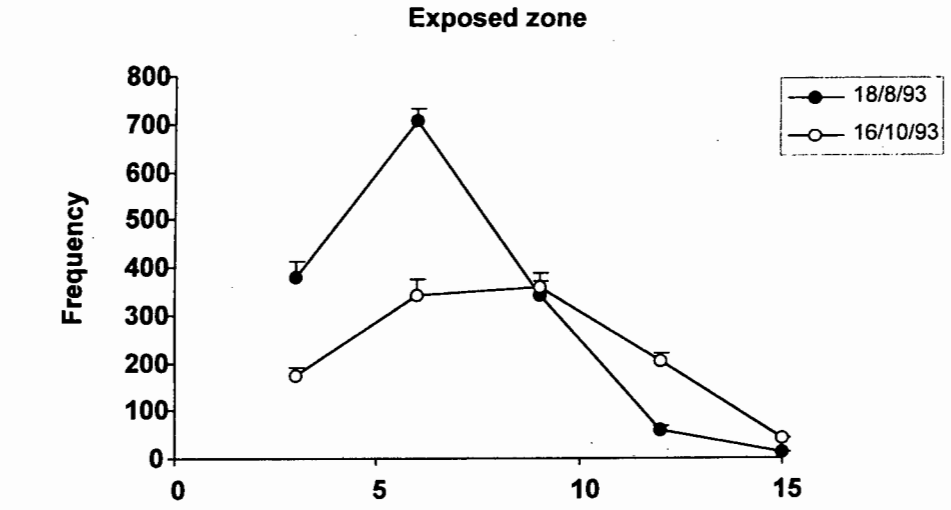
2. Recruits

The fact that this data set was collected over a short time period precluded it from being analyzed by cohort analysis techniques. Also, more or less all size ranges of a population need to be represented to enable the growth parameters (and hence mortality) to be estimated. Nonetheless, one can compare the differences in the average size of individuals in cohorts over the two months to get a measure of growth with respect to wave action.

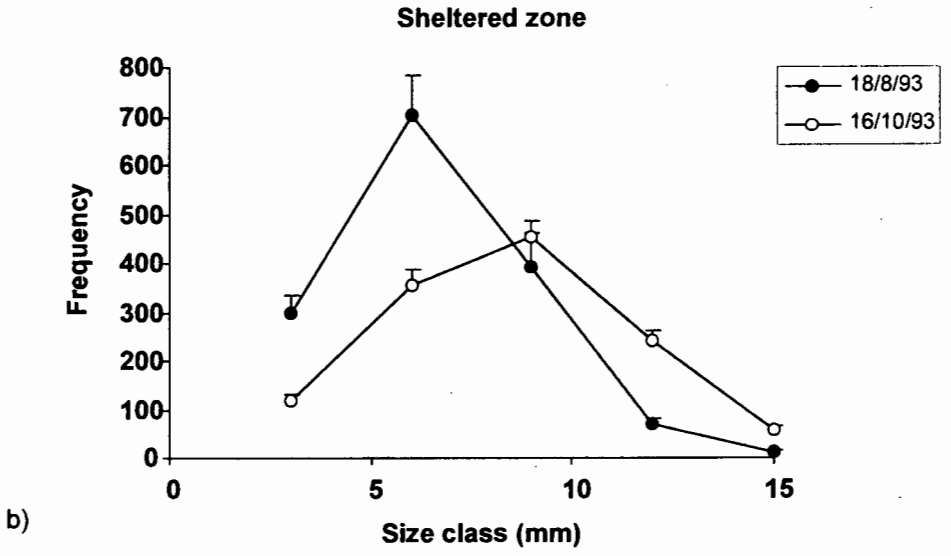
The measurements were converted to size-frequency data and can be referred to in Table 3.2. Note that the total numbers of recruits in the sheltered and exposed zones are approximately equal and this is true across all size classes. The difference in average size of cohorts over the two month period is 1.9 mm for the sheltered zone and 2.0 mm for the exposed zone. This infers similar growth rates between the two zones, irrespective of the degree of wave exposure. The similarity in numbers of individuals per size class between zones for both months is indicative of comparable growth and mortality rates. Because a growth curve could not be estimated, it is impossible to establish what proportion of the loss of individuals in a size class represents mortality and what proportion has grown to the next size class. The graphical presentation of the data (Figure 3.1) reveals the remarkable parallelism of the two zones over this short time period.

Table 3.2 Frequency of recruits (and standard deviations in brackets) in 3 mm size classes for the sheltered and exposed zones. The average sizes of mussels is also given as an indicator of growth.

	Sheltered zone		**Exposed zone**	
	18/8/93	16/10/93	18/8/93	16/10/93
0 - 3 mm	300 (35)	117 (15)	378 (36)	173 (18)
3 - 6 mm	701 (83)	357 (33)	706 (28)	343 (31)
6 - 9 mm	392 (68)	455 (31)	341 (30)	357 (29)
9 - 12 mm	71 (12)	242 (20)	59 (10)	202 (16)
12 - 15 mm	14 (2)	56 (8)	11 (0)	41 (3)
Total	1478	1227	1495	1116
Average size	5.5 mm	7.4 mm	4.5 mm	6.5 mm



a)



b)

Figure 3.1 Size frequency distributions of recruits for the exposed and sheltered zones. The data were collected over a two month interval. The "modal" progressions are indicative of growth and/or mortality.

3 Cohort analysis of the full size range of mussels

3.1 Exposed zone

The growth parameters estimated for the high and low shores after hypothesis testing (at levels described above) are summarized in Table 3.3. The von Bertalanffy growth parameter, K is calculated for the year and the objective function represents the log-likelihood value of the best fit. Of particular interest is that animals on the low shore did grow faster than those on the high shore, but the difference is small. It is important to note that the L-infinity for the high shore has been overestimated and that this has consequences for the von Bertalanffy K value. The two parameters are obviously related and as a result, K is deflated. This implies that the differences related to tidal levels are more modest. The distributions, with normal curves fitted to all of the cohorts detected, can be viewed in Figure 3.2. - distributions for every month sampled have been mapped for each site.

Table 3.3 Growth parameters estimated from length-frequency data for the exposed and sheltered zones. The best log-likelihood function is also given for each analysis.

	Exposed zone		Sheltered zone	
	Low shore	**High shore**	**Low shore**	**High shore**
K (1/year)	0.195	<= 0.095	0.181	0.044
L-infinity	92.6 mm	99.7 mm	124.6 mm	181 mm
No. age classes	6	5	6	5
Objective fn.	2662	1613	2636	1461

3.2 Sheltered zone

The growth parameters computed for the high and low shores are presented in Table 3.3 above and the distributions are graphed in Figure 3.2. The results of the two analyses indicate that the growth rate of low shore animals is far greater than that of the animals residing higher up. These results are in agreement with those obtained by labeling individual mussels. However, the L-infinity estimated for both shores is exaggerated (markedly so for the high shore) and the von Bertalanffy K values for each have therefore been underestimated. The overall patterns are nevertheless worth noting, but further interpretations of the absolute values have been kept short.

Of further interest is that the growth curve parameter for the exposed low zone only slightly exceeds that for the sheltered low zone. These results mirror the outcome of the previous data analysis, in which differences between these two sites were statistically insignificant. Growth rates are nevertheless reliant on the relative position on the shore, but these rates are only notably different for animals inhabiting the sheltered, high shore.

3.3 General patterns : exposed and sheltered zones

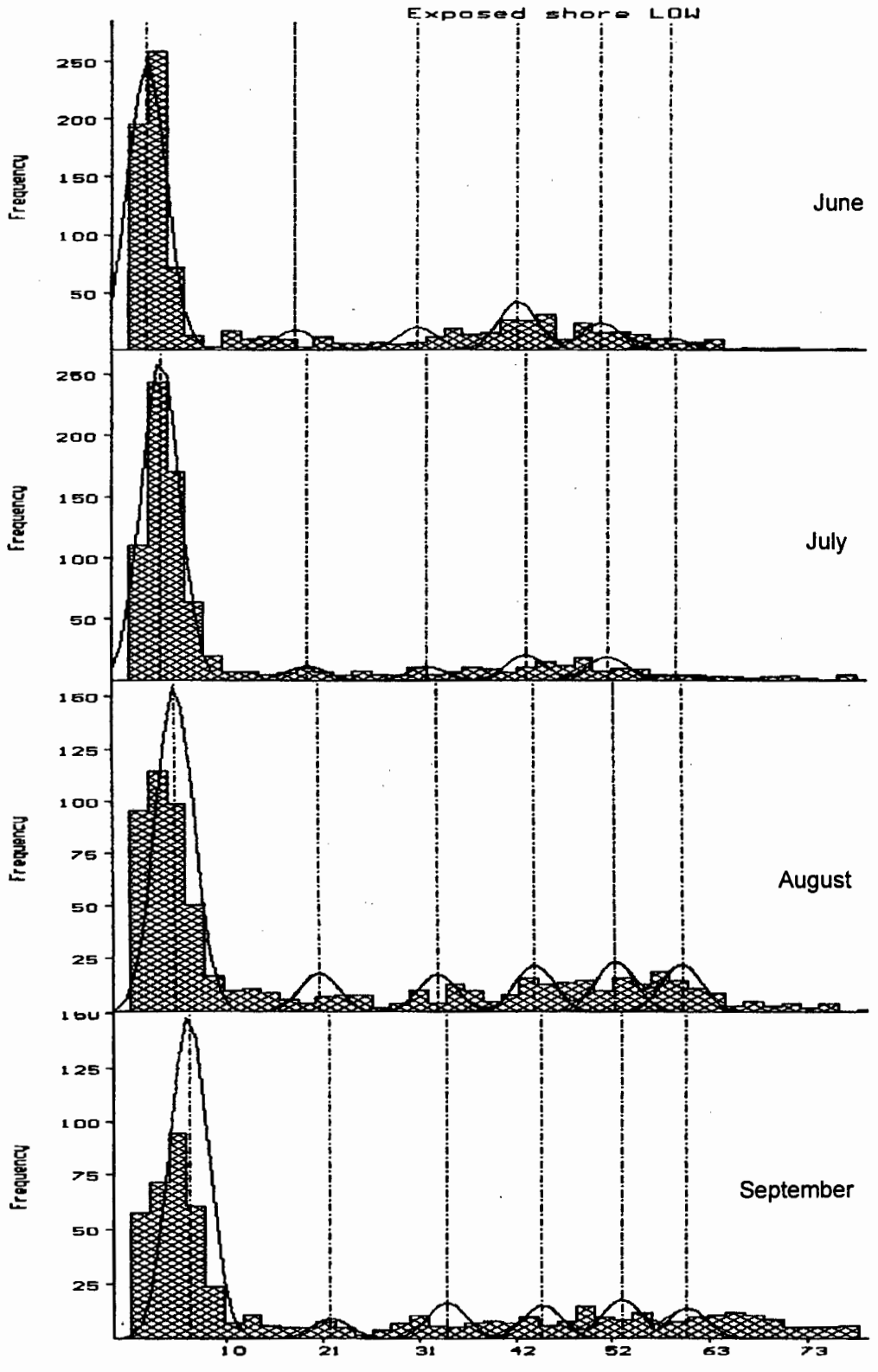
Additional interesting inferences may be derived from the MULTIFAN analyses which are summarized in Table 3.4. The maximum size recorded for the exposed low zone exceeded that for any zone (± 95 mm). Next was the size recorded for the sheltered low zone (± 89 mm) followed by the exposed high zone (± 62 mm). Mussels in the sheltered high zone reached a maximum size of approximately 53 mm. These data reflect (to some extent) the von Bertalanffy growth parameter estimated for each site because growth rates are often proportional to the maximum size achieved by animals. Branch (1976) established this relationship for the South African limpet *Patella granularis*.

Table 3.4 Maximum size (in millimeters) achieved by mussels in exposed and sheltered areas, average number of recruits (per 100 cm^2) in the first cohort and relative survival of this cohort. All results have been estimated from length-frequency distributions (Figure 3.2).

	Exposed zone		**Sheltered zone**	
	High shore	**Low shore**	**High shore**	**Low shore**
Maximum size	62	95	53	89
No. of recruits	250	175	80	30
Survival	low	very low	high	low

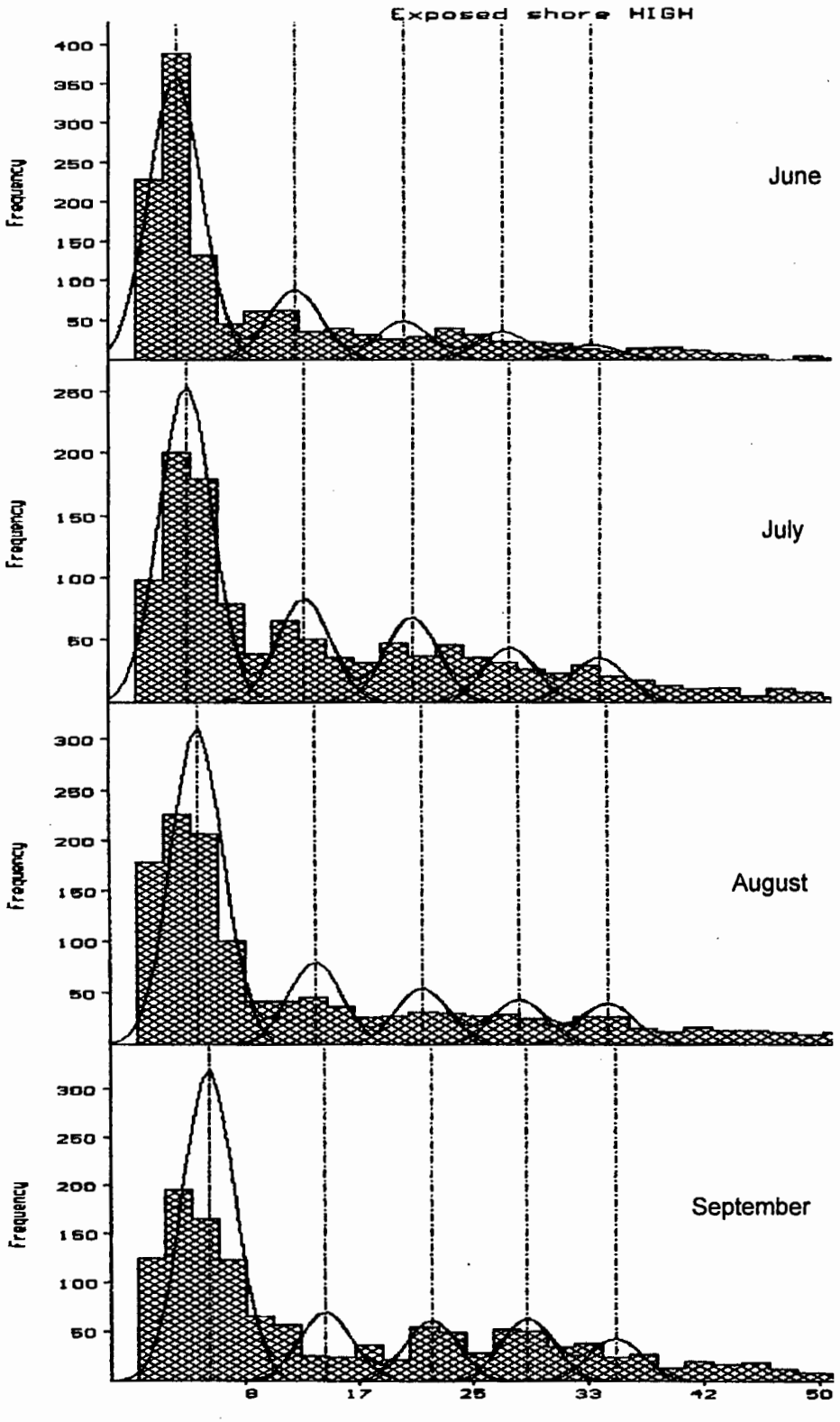
The relative recruitment intensity at each site is also estimable from the first cohort of the length-frequency distribution (Figure 3.2) and two general patterns emerge: 1) the exposed area experienced higher recruitment than the sheltered area and 2) the high zones in the each area acquired more recruiting mussels than the low zones. More specifically, recruitment was (on average) approximately three times as great in the exposed high zone than the sheltered high zone. The sheltered low zone had fewest recruits, averaging around 30 per unit area for the four months. These trends follow the patterns established for all recruits (0 - 15 mm) in chapter one and these are explored further in chapter two.

Mortality of the first cohort, as depicted in Figure 3.2 is exceptionally high at the exposed low and high sites. The distribution plot for the sheltered low zone suggests erratic recruitment in this area and survival of the first cohort was low relative to that exhibited by cohorts 4, 5 and 6. Survival of cohort 1 is comparatively high in the sheltered high area.



a)

Figure 3.2 (a-d) continued on next page



b)

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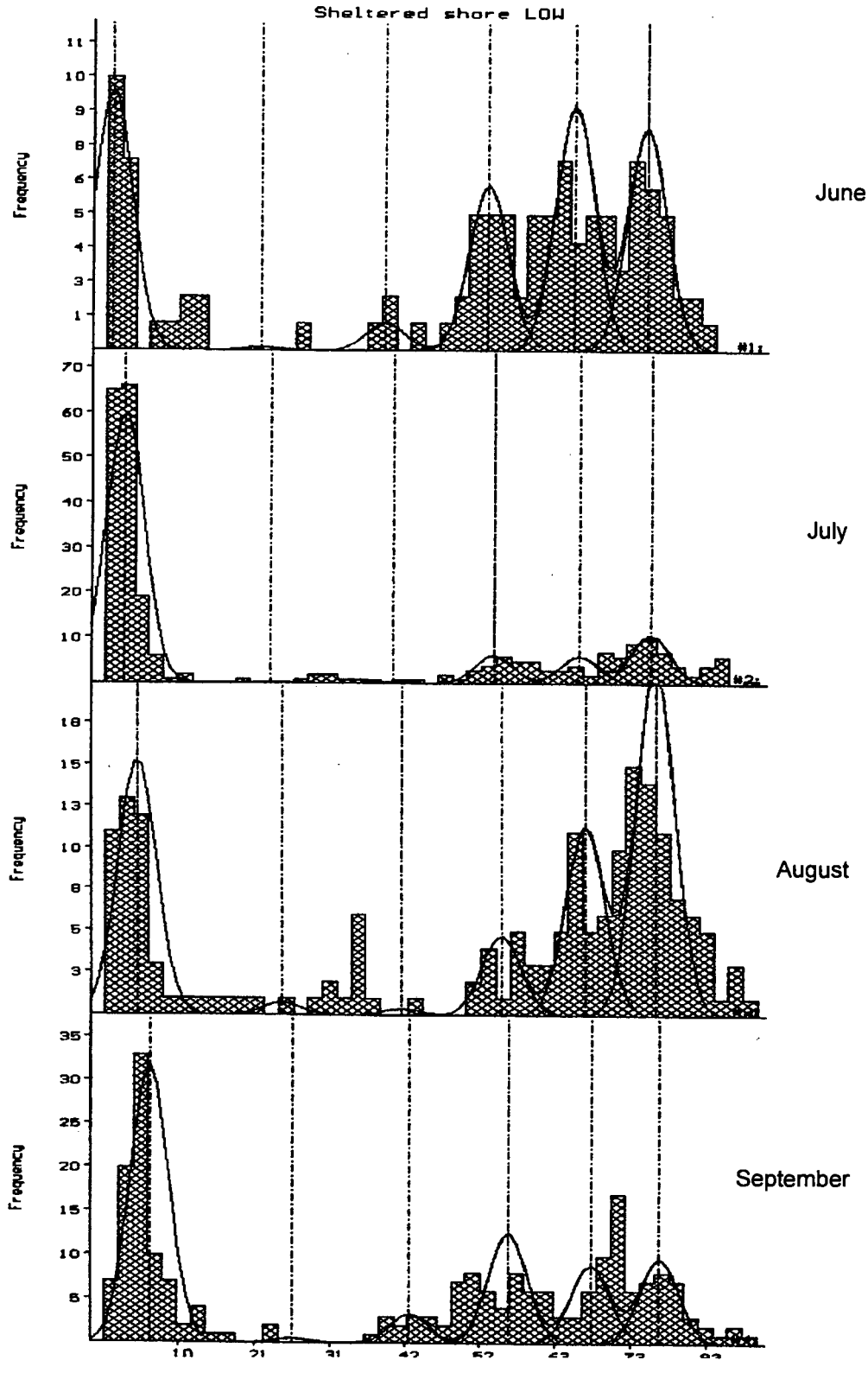

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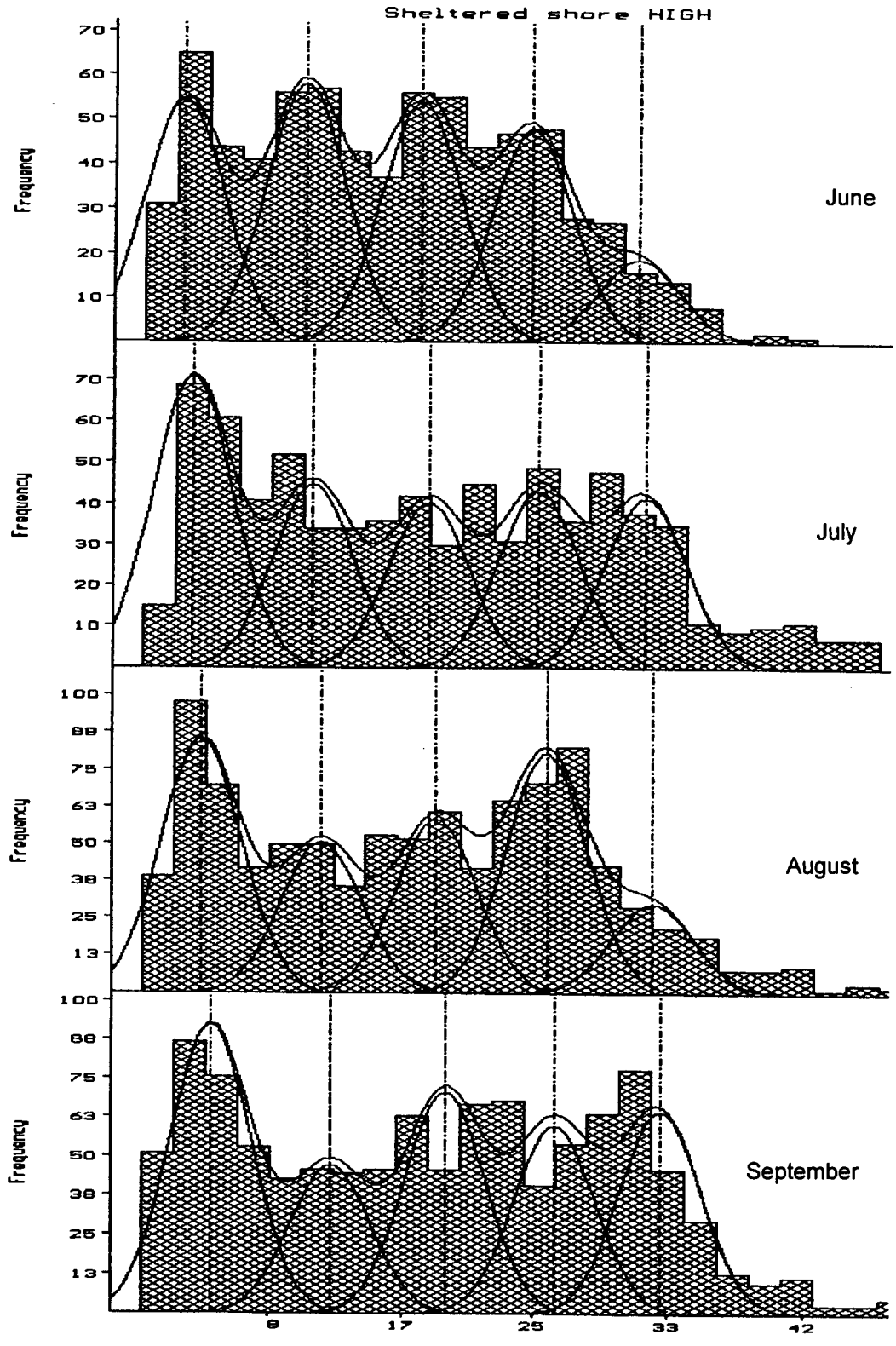


d)

Figure 3.2 Length (mm) frequency distributions of mussels collected from exposed and sheltered, high and low shore sites in Camps Bay, from June to September 1993. Frequences represent numbers of individuals / 0.06 m^2.

3.4 Exposed and sheltered zones - recruits

It is uncertain whether the modes of the larger animals detected by MULTIFAN represent true cohorts (see Figure 3.2). By comparison, normal curves fitted to the first cohort do seem reliable and these have been extracted to compare the growth rates of young mussels at each site. The mean lengths of the first mode are plotted for the months of June - September 1993 (Figure 3.3). An analysis of covariance was not used to test homogeneity of the y-intercepts because the regression slopes are heterogeneous ($n = 16$, $\alpha = 0.05$, $p < 0.001$, SYSTAT v 5.0). The graph illustrates that mussels on the low shores grew faster than those residing on the high shores for both sheltered and exposed zones. Furthermore, mussels at the sheltered high site grew much slower than other mussels. This confirms the previous findings.

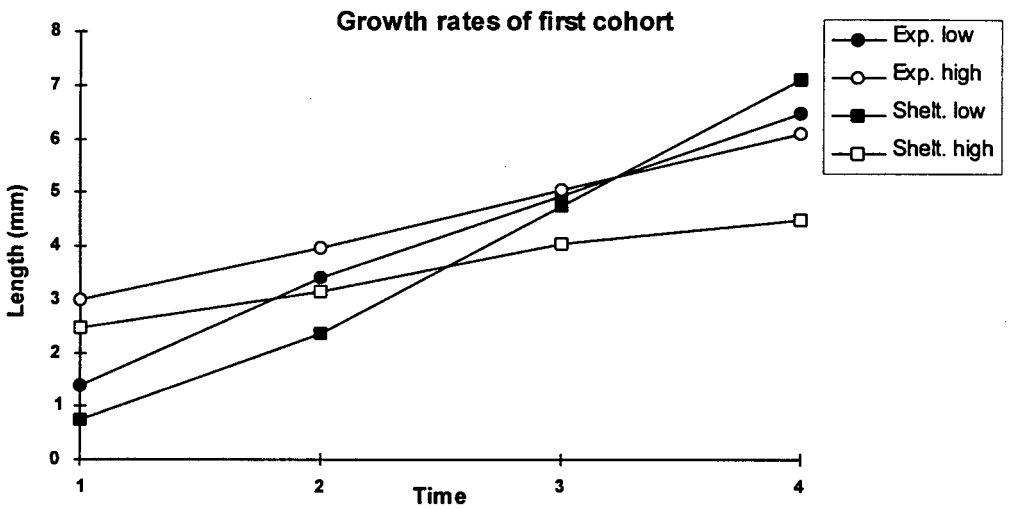


Figure 3.3 Growth rates of young mussels in sheltered and exposed areas, spanning the period June - September (times 1 - 4). The means of the first modes have been estimated from MULTIFAN analyses on the full size range of mussels (see Figure 3.2).

DISCUSSION

Growth of the exposed, high-shore adults was faster (on average) than at any of the other three sites and this may be attributed to a) the enhanced ability to acquire nutrients in a wave-exposed area and b) the smaller size of these individuals compared with those on the exposed low shore. Animals that are smaller tend to grow faster than larger animals (e.g. von Bertalanffy 1957, Griffiths and King, 1979). The only statistical difference in growth rate, however, was exhibited by mussels inhabiting the high shore in the sheltered zone, which grew slower than mussels at any of the other sites.

The finding that (tagged) mussels from the sheltered, high shore grow significantly slower than those on the sheltered low shore is hardly surprising given that they receive less water and therefore have less feeding time than those situated further down. Griffiths (1981) found that growth rates of *C. meridionalis* declined markedly with increasing shore height. At the Seafarm culture facility in Saldanha Bay, van Erkom Schurink and Griffiths (1993) found that increasing levels of tidal exposure retards growth in *M. galloprovincialis* and this was also established for all 3 indigenous South African species of mussel. The interesting outcome of this study was that although all species exhibited slower growth at increasing tidal exposure, *Mytilus* did not exhibit huge drops in growth rates but was capable of maintaining analogous growth rates over a range of conditions. Griffiths *et al.* (1992) had previously found *M. galloprovincialis* to show an enhanced tolerance to desiccation compared with the indigenous South African mussels. That *Mytilus* is exceptionally robust in terms of its response to varying environmental conditions is also apparent from the outcome of experiments on circulation rates - its growth was only slightly inhibited in the sheltered zone. The hardiness of this species would explain the current findings that while animals on the sheltered high shore grow more slowly than at any of the other three sites, no other significant differences in growth rate are apparent (for tagged animals). An alternative explanation might be that the physical differences in the environment were not severe enough to result in large divergence in growth rates. A long-term study combined with physical measurements of the relevant environmental variables would be appropriate in answering these questions. Moreover, there are a number of confounding factors that might affect growth and these are discussed below.

An additional factor that may be responsible for habitat-related size differences observed in *M. galloprovincialis* is that densely packed mussels are limited for space and can't grow freely in all directions. These mussels tend to be thinner than animals that have more space available to them but they may achieve greater lengths (all else being equal). In the exposed zone (particularly on the low shore) at Camps Bay, *Mytilus* beds are multilayered and are generally densely packed. Mussel beds in sheltered areas tend to form a single layer only and are less densely packed. There are in fact about twice as many mussels per unit area in the exposed

zone than there are in the sheltered zone (see Chapter one). Seed (1969) reported that shell shapes of mussels vary according to the growth conditions and population density. *M. galloprovincialis* shell shapes are known to vary even between populations that are close together (Raubenheimer and Cook, 1990) and so the differences found in Camps Bay, where conditions do vary over short distances are not unexpected.

Another environmental factor known to affect growth is the level of sand inundation experienced by mussels. *M. galloprovincialis* in particular grows more slowly in high silt conditions (van Erkom Schurink and Griffiths, 1993) although *C. meridionalis* grows faster in similar conditions. Animals in sheltered areas in Camps Bay were more heavily eroded than in other sites (pers. obs.), suggesting a greater degree of sand-scouring. Some of the animals at this site experienced what seems to be negative growth. The negative difference in lengths range from 0.5 mm to 4.2 mm but there was usually only a difference of 1 mm. It is noteworthy that animals in the low region of the sheltered zone exclusively showed such negative growth. It seems most likely that the shells of these animals have been eroded by sand-scouring during the four months - during collections it was also observed that animals in the sheltered low area were relatively easy to remove because of the build up of sand between mussel and rock. "Negative" growth due to erosion has been found to occur in the South African limpet *Patella argenvillei* on the west coast (S. Eekhout, pers. comm.) and this phenomenon should not be surprising considering the exposed nature of the coastline. Alternatively, the discrepancy could be due to human error when measuring the animals, since at time zero the mussels were still attached to the rocks and some difficulty was experienced in positioning the calipers at the base of the shell. It is, however, unlikely that a discrepancy of 4.2 mm would have been made in this way, or that such errors would have been confined to the low, sheltered site.

By comparison with investigations on growth of *M. galloprovincialis* by van Erkom Schurink and Griffiths (1990), the growth performance of adult *M. galloprovincialis* at all sites in this study was remarkably slow: cultivated mussels, having an initial length of 20-40 mm attained a length of 55-90 mm within four to five months. The fastest growth attained by adult mussels in the present study was 4.43 mm in four months. These differences in growth only emphasize the dependency on habitat since cultivated mussels are usually grown on ropes or similar structures that are always submerged. These mussels not only have more available feeding time, but do not have imposed on them the stresses of dehydration or desiccation. Indeed, intertidal mussels of all four South African mussel species are smaller than subtidal mussels due to reduced feeding time (van Erkom Schurink and Griffiths, 1990). Ceccherelli and Rossi (1990) explored the growth rate of *M. galloprovincialis* in its natural habitat on the Adriatic coast. In this region *Mytilus* is found subtidally, on the muddy bottom of a lagoon. Growth

was fairly rapid and newly settled mussels grew to 50 mm within 14,5 months. The authors also found that this rate of growth was lower than that achieved by cultivated mussels. In another study by Lubet (1974 in Berry, 1978), *M. galloprovincialis* grew between 15 and 32 mm per year in their natural habitat. It is evident that a description (and quantification if possible) of the environment in studies of this nature is critical if one wishes to make valid comparisons.

The growth (and mortality) of recruits followed over two months was remarkably similar in the sheltered and exposed zones at Camps Bay. In both regions, young mussels grew approximately or exactly 2 mm. Of note is that these data were collected from the low shore only and no comparisons could be made with respect to height on the shore. It would also be interesting to follow the growth and mortality of young mussels for a longer period to see whether any differences would emerge over lengthy periods.

The analysis performed on the numbers of lost (tagged) mussels show that mortality rates in the intertidal region is site-dependent and related to the degree of wave exposure and tidal height. In order of increasing mortality, the results for the sites were sheltered high (20%), exposed high (32%), sheltered low (47%) and exposed low (91.5%). The ANOVA performed on the numbers of unrecovered mussels expresses that, statistically, the exposed low shore experienced a significantly higher rate of mortality than the remaining sites. The sheltered low shore was found to be significantly different to the sheltered high shore and no other statistical differences were detected. The variance in mortality at different positions on the shore reflects the subjectively determined environmental differences at these sites. The exposed low shore at Camps Bay experiences considerably high wave energy by comparison to the remaining three sites and it was almost always difficult to gather data from this area. Differential mortality, related to habitat conditions has been found elsewhere in natural populations of this mussel. Ceccherelli and Rossi (1990) reported that the higher mortality rates of *M. galloprovincialis* during spring-summer were probably due to excessive amounts of detritus during this period. No previous studies on mortality have been carried out where this species occurs naturally in South Africa, but on the high shore, desiccation rather than wave action would seem to determine densities of *M. galloprovincialis*. Having said that, in relation to other mussels, *Mytilus* is relatively tolerant to desiccation - this is borne out by the fact that *Mytilus* beds extend further up the intertidal zone than any other South African species of mussel (Griffiths *et al.*, 1992).

It should be mentioned again that the controls that were set up to detect lost labels as opposed to dislodged animals gave clear results in that no labels were lost. Nonetheless, the design of the controls may be improved upon to allow unequivocal interpretation of the

relevant losses - "control" animals should be glued to the substrate in such a manner that the angle at which they lie is comparable to that of naturally attached animals. Animals lying flat against the substrate, as was the case with these controls, might not lose any (or few) tags while upright animals that experience the full force of the waves are more likely to lose their labels. Clearly, the packing density of mussels will also interfere with the degree of force experienced by a mussel and such differences will not be accounted for in the design used here.

The results obtained from the MULTIFAN method (on the full size range) are that animals residing in the sheltered high shore show notably depressed growth rates. The difference in growth rates between the exposed low and high shores and the sheltered low shore are minimal. The outcome of the cohort analyses are in accordance with the patterns that emerged from tagged adults. This is so, despite the fact that the MULTIFAN method was performed on all size categories of *Mytilus*. When growth rates of the first cohorts were further analyzed, the depressed growth rate of mussels from the sheltered high shore was again conspicuous. Young mussels at sheltered and exposed low sites also exhibited faster growth than those from high shore sites but these data could not be tested statistically. What is conspicuous from these analyses is that growth of mussels does depend on habitat differences, which is not an unusual phenomenon (see e.g. van Erkom Schurink and Griffiths, 1990; Berry, 1978; Du Plessis, 1977; Griffiths, 1981; Crawford and Bower, 1983). This study confirms that these differences can emerge within a relatively small area.

The actual values of the von Bertalanffy growth parameters are, however, questionable for reasons that are discussed below. While all fits have undergone hypothesis testing and are therefore significant at the levels stated earlier (*sensu* Fournier *et al.*, 1990), attention should be drawn to the L-infinity value estimated for both the sheltered and exposed high shore data. High shore animals do not attain this length (regardless of wave exposure) and this parameter has clearly been overestimated. The result of the high L-infinity values is that the slope of both growth curves, K, have been underestimated. The tendency of MULTIFAN to produce depressed values of K has been reported elsewhere. In a study of the growth of horse mackerel, Kerstan (in press) reported that MULTIFAN produced unrealistically low values of K and excessively high L-infinities as a result of an overestimation of the number of age classes.

All methods of cohort analysis have been criticized for their limitations (see for example Isaac 1990, Martin and Cook 1990, Jones 1990) and MULTIFAN is no exception. Terceiro *et al.* (1992) found that MULTIFAN is not well suited to deal with populations that spawn continuously or in multiple events - estimates of growth will therefore not be accurate for these populations. It is obvious from the present investigation that *M. galloprovincialis* exhibited

recruitment over the entire four months of observation, since animals of 2 mm were always present (see Figure 3.2) and at Groenrivier on the west coast *M. galloprovincialis* recruits year-round, although there are peaks of settlement (Branch, pers. comm.). This is likely to have been a cause of unreasonable estimations of L-infinity for the low and high shore animals and it is possible that the growth parameters of the analysis performed on the sheltered and exposed zone data are also depressed. While the survey sample parameterisation of MULTIFAN (Fournier *et al.* , 1990) estimates total instantaneous mortality rates, the assumption that all cohorts experience the same age-independent total mortality is not met by *Mytilus* and this analysis could not be performed on the data. This was confirmed when a test run of the sample survey method on the exposed data set produced an L-infinity of over 3000 mm and the analysis was stopped at this point. General patterns of mortality of young mussels were nevertheless extracted from the distribution plot and deserve mentioning. Survival of the first cohort in the low shore of both sheltered and exposed areas is extremely low but is relatively high at the sheltered high site. Mortality is higher in the sheltered low shore but is low compared with both exposed sites. The zonational patterns of mortality in young mussels mirrors the differential survival of tagged adults and corroborate the suggestion that mortality rates are indicative of the strength of wave action at these sites.

There are a number of ways in which the MULTIFAN parameter estimations could be improved upon: the larger the sample size, the more accurate the estimates are likely to be (see Fournier *et al.*, 1990) and data collected over a longer time span would provide refined results. One can also increase the reliability of the parameters estimated by aging the animals and incorporating these data into the model (Fournier *et al.*, 1990). In fish this is often done by examining the otoliths (e.g. Kerstan, in press) and it is not unrealistic to advise that mussels be aged equally objectively (even if it involves a labour intensive mark-recapture technique).

Despite the shortcomings of MULTIFAN, the patterns that have emerged from the analyses are in agreement with the analyses performed on tagged animals. There is no denying that the growth parameters need to be re-estimated with a more appropriate data collection and then, to use these parameters for stock assessment or for providing estimates for exploitation purposes. A final comment on the methodologies employed to infer growth is that although the use of tagged animals inevitably leads to pseudoreplicated data (see e.g. Underwood, 1981, 1990) it is (when applied properly) likely to yield more accurate measurements of growth than cohort analysis, when additional aging data are unavailable.

Wave action has long been recognized as an important factor in determining community structure and dynamics (e.g. Ballantine, 1961; Jones and Demetropoulos, 1968; Seed, 1969; McQuaid and Branch, 1985; Delafontaine and Flemming, 1989; Gaylord *et al.*, 1994).

Because species are sensitive to their environment, some authors have proposed a biological scale which would reflect wave exposure at a particular site (e.g. Ballantine, 1961; Lewis, 1974). This method has a number of flaws, one of which is that confounding factors such as topography may also come into effect. In addition, the assumption that community patterns respond in a linear fashion to wave action is objectionable - many species show a unimodal response to an environmental gradient (Jongman *et al.*, 1987). Subjective estimates of wave exposure are considered to be acceptable (e.g. Jones and Demetropoulos, 1968) but there is the danger of expressing the association of community structure with environmental variables in a circular fashion. Another important factor worth considering, and pertinent to this study is that it is difficult to separate the effects of wave exposure and shore height because clearly the two go hand in hand - an area high up on the shore will not experience the same hydrodynamic forces as an area lower down (see for example, Bustamante,1994). It is impossible to know subjectively whether the sheltered low site at Camps Bay experiences markedly different hydrodynamic forces to the exposed high site or how this varies temporally. Both wave action and aerial exposure ought to be quantified - when analyzed in conjunction with population data (using multivariate statistics such as direct gradient analysis), one might determine which environmental variable/s or combination of variables are responsible for the patterns that emerge on the shore. Comparisons of the nature of the present study are possible but further interpretation must be treated prudently until values are obtained for the relevant environmental parameters.

CHAPTER 4

What are the reates of disturbance of mussel beds under different conditions of wave action and zonation?

How do these relate to strength of byssal attachment?

INTRODUCTION

The importance of physical disturbances in structuring biological communities has long been recognized (Levin and Paine, 1974; Connell, 1978; Sousa ,1979; Paine and Levin 1981, Connell and Keough, 1985; Ebeling et al., 1985; Witman, 1987) and is one of the reasons that ecological systems are highly dynamic. The frequency, magnitude and timing of disturbances all contribute to the type of change that occurs (see Sousa, 1985; Petraitis *et al.*, 1989), with the result that the dynamics of biological systems are difficult to predict. Disturbances often create open patches, which may be at different successionary stages in a particular landscape, depending on their age. The types of stochastic physical disturbances experienced in marine communities are extensive. Tidepools may be disturbed by wave action, excessive heat and wave-driven logs or rocks (Dayton, 1971; Dethier, 1984). Intertidal biota are often affected by sand inundation (Taylor and Littler, 1982; Littler *et al.*, 1983) or an unstable habitat e.g. boulder fields which are overturned by waves (Sousa, 1979). Ice-scouring has frequently disturbed the rocky coast of Massachusetts in the historical past (Wethey, 1985). Heavy storms and associated wave action commonly affect marine flora (Ebeling *et al.*, 1985) and fauna - mussel beds providing the focus of many studies (e.g. Levin and Paine, 1974; Asmus, 1987; Witman, 1987; Nehls and Thiel, 1993). Such disturbances are often the cause of severe mortality. Storm-related disturbance is probably the most important external factors contributing to the organization of intertidal systems, partly because its effects are often dramatic and abrupt. The spatial scale on which these disturbances act may be localized or they may manifest themselves on a relatively large, regional scale. Disturbances associated with storms and heavy wave action occur frequently or infrequently and vary seasonally, winter storms being more common along most temperate coasts (Sousa, 1985).

In the winter of 1993, following severe storms typical for this time of the year, a large area of mussel bed was dislodged from the exposed low zone at the Camps Bay study site. By coincidence, permanent plots had previously been set up in the area on 5 - 10 April to monitor the relative growth of mussels at sites which experience different grades of wave action (see Chapter 3). Six replicate plots per site, with an area of 900 cm^2 each, had been cleared of mussel bed in both low and high zones in sheltered and exposed areas. Nails had been drilled into the granite rock and were labelled with cable ties so that the plots were marked permanently for future observation. Severe storms then beset the west coast, prohibiting research during this period and the growth plots were revisited during spring tides from 2nd - 7th June. At this time, only the nails and ties provided signs of where the mussel bed had been manually cleared in the exposed low zone because storm-induced wave action had dislodged the better part of the mussel bed.

This unexpected turn of events provided an excellent opportunity to investigate the "uprooting" of mussel beds commonly observed on wave-exposed coastlines. Both the position and size of the patch were noteworthy and provoked the current investigation. The question of the position of the patch is two-fold. Firstly, while the exposed low zone was almost completely denuded of mussels, the exposed high zone appeared relatively unaffected. Similarly, both high and low-shore sheltered sites showed little sign of storm damage. Secondly, the areas affected by the storms were immediately adjacent to the manually cleared "growth" plots - mussel bed that was not experimentally interfered with seemed to have been unaffected by the storms.

It seemed possible that the key to these findings resided in the relative attachment strength of mussels at these various sites, raising questions about the variability of byssal attachment strength and its relationship to environmental pressures. Of particular interest was whether the strength of byssal attachment differed, a) between experimental sites, which experience different grades of wave exposure and are at different tidal elevations, b) with the position of the mussel, i.e. whether or not a mussel lay adjacent to a previously cleared patch ("edge effect") and c) temporally. More specifically, with respect to these three variables, it was hypothesized that a) differences in attachment strength might vary in sites experiencing different amounts of wave action; b) mussels situated on the edge of cleared areas would be initially more vulnerable to wave action because their attachment would be weakened and they would lack protection of neighbouring mussels; 3) with time, these "edge" mussels would compensate by becoming more firmly attached.

MATERIALS AND METHODS

1. Quantification of denuded area

To quantify what area was disturbed at each site (exposed low and exposed high, sheltered low and high shores), photographs of each of the cleared growth plots (three per site) and their immediate surrounding area were taken on the 2nd - 7th June 1993, soon after the storms had struck. The field of view of each image was approximately 4730 cm^2, comprising the 900 cm^2 growth plots and the surrounding area (e.g. 3800 cm^2). The photographs were digitized and analyzed with a Joyce-Loebl (micro-magiscan 3) image analyzer and Pentax smc pentax-f 50 mm macro lens. Prior to the storm, none of the growth plots was surrounded by bare rock; after the storm, the area surrounding each plot was quantified in terms of whether there was bare rock, mussels, macroalgae or barnacles[2]. The area of bare rock was

[2] See Chapter one for details - this method is similar to that used for measuring mussels, except that calculations are based on varying shades of grey, depending on the substrate type.

calculated from the digitized photographic image using M3Genias v 2.1 software. This measurement represents the area of dislodged mussel bed only, as was evident by the byssus threads that were left behind, and specifically excludes the 900 cm^2 growth plot that was experimentally cleared.

The entire exposed low shore was also captured in a single photograph and this was used to measure the total area of mussel bed removed at this site. The area of denuded rock was traced from an enlarged projected image and the drawing was scanned with an Omnimedia Scanner XRS and Adobe Photoshop 2.5.1 software package for MacIntosh. The digitized image was calibrated and analyzed with NIH Image 1.53b55 software for MacIntosh. Estimates were also made of the total areas of mussel bed removed from the other three sites.

2 Measurement of attachment strength and length

Individual mussels were plucked from the rock using a device consisting of either a crocodile clip or a battery clamp attached to a spring balance, allowing measurement of the strength of byssal attachment. This method is comparable to that used by Harger (1970) and Price (1980, 1982). The original measurements were converted from kilograms to Newtons by multiplying values by 9.81. Shell lengths were recorded concurrently, being measured to the nearest millimeter with vernier calipers.

A two-way analysis of variance (ANOVA) was performed on the force data to determine whether strength of attachment varied according to the site at which animals are located, and whether there was a temporal effect. Additionally, a two-way ANOVA tested for significant differences in shell length between sites, at different times. SYSTAT v 5.0 statistical software was employed for both analyses. MANOVA was not employed for these data in view of the fact that shell length and attachment strength are not independent variables (see also results of linear regression, Figure 4.2).

Shell length and strength of byssal attachment recorded (coincidentally) at the time of plot clearance, and two weeks later, were regressed for a) animals residing within the mussel bed, and b) mussels located on the edge of plots using Excel for Windows, v 5.0. The linear regressions would reveal what relationship occurs between the two variables, under different conditions.

3 Experimental conditions

In March 1993 experimental plots were set up to simulate the clearing of the original "growth" plots prior to the storm damage (see Chapter 3). Three (30 x 30 cm) replicate plots were cleared of mussels from the high and low zones in exposed and sheltered areas using a paint peeler at each site.

To test for the "edge effect", measurements of attachment strength were made for ten mussels situated on the edge of each simulated growth plot (three per site) and for ten positioned in the centre of the mussel bed surrounding these plots. An initial collection was made at the time of clearance of the plots.

A second set of force and length measurements was taken for animals within the mussel bed and on plot borders, two weeks after the original data collection to test for temporal changes in attachment strength.

SYSTAT (v 5.0) software package was used to perform analysis of covariance on the length-force data for the exposed high site and the exposed low site, and similarly for both sheltered sites. Both initial and final length-force data were analyzed for individuals within the mussel bed and on plot edges, therefore generating four "treatments" per analysis (initial mussel bed, final mussel bed, initial edge, final edge). Data were tested for homogeneity of variances, and outliers were subsequently removed to comply with this criterion. Normal probability plots confirmed that the data were sufficiently normally distributed.

RESULTS

1. Quantification of disturbed area

The areas disturbed by wave action within each fixed quadrat at each site (treatment) appear in Table 4.1. It is clear that the exposed lower zone was affected to a far greater extent than any other site, experiencing a mean loss of 46% per quadrat. The exposed high site experienced a slightly higher loss of mussel bed than either of the sheltered sites, but this was significantly less than the area disturbed at the exposed low site.

Table 4.1 Area of bare rock calculated for four intertidal sites, from digitized photographs of the fixed quadrats. There are six replicate quadrats per site; the average area disturbed for each site is given in bold with its mean percentage loss.

Exposed zone		Sheltered zone	
Low shore	**High shore**	**Low shore**	**High shore**
1110 cm^2	895 cm^2	186 cm^2	972 cm^2
2268 cm^2	718 cm^2	267 cm^2	181 cm^2
2145 cm^2	98 cm^2	334 cm^2	143 cm^2
2026 cm^2	670 cm^2	241 cm^2	380 cm^2
1587 cm^2	150 cm^2	364 cm^2	232 cm^2
1362 cm^2	71 cm^2	439 cm^2	191 cm^2
1750 (46%)	**434 (11%)**	**305 (8%)**	**350 (9)%**

The one-way ANOVA revealed a significant difference in the four treatments ($n = 24$, $\alpha = 0.05$, $p < 0.001$). Tukey's HSD simultaneous pairwise comparisons test confirmed that the amount of disturbed area in the exposed lower site was significantly greater than in the exposed high, sheltered low and sheltered high sites (experimentwise error = 0.5, $p < 0.001$ in all cases) and that none of the other pairs were statistically different to each other ($p > 0.9$).

The total area of mussel bed disturbed by the storms in the exposed low zone amounted to 1.4 m^2, whereas that disturbed in the other three areas was estimated to be less than 0.27m^2.

2 Attachment strength and shell length

Length and force measurements for all subsequent analyses appear in Tables 1 and 2 (see Appendix). The mean attachment strength and shell length have been calculated for each site to provide an indication of their relative values. Data recorded in these tables have been summarized in later tables, where appropriate.

2.1 Between-site comparisons

Between-site comparisons of attachment strength revealed that mussels were more firmly attached at the exposed low site than at the remaining three sites, both at the time of clearance and two weeks thereafter (Table 4.2). Mussels at the sheltered low site were always more firmly attached than those at both high shore sites, and mussels at the sheltered high shore site always had the weakest attachment strength.

Table 4.2 Average attachment strength (N) and length (mm) of animals collected from the intact mussel bed. Figures comprise measurements taken at the time of clearance and two weeks later. Standard deviations are given in brackets and the range of lengths at each site is given in bold in the last row of the table.

	Exposed zone				**Sheltered zone**			
	High shore		**Low shore**		**High shore**		**Low shore**	
	Initial	**Final**	**Initial**	**Final**	**Initial**	**Final**	**Initial**	**Final**
Force	33 (10)	36 (13)	52 (23)	59 (17)	18 (9)	27 (10)	43 (16)	55 (17)
	n = 30	n = 30	n = 30	n = 30	n = 30	n = 30	n = 30	n = 30
Length	44 (5)	42 (7)	63 (14)	65 (8)	37 (5)	37 (4)	66 (7)	66 (7)
	n = 30	n = 30	n = 30	n = 30	n = 30	n = 30	n = 30	n = 30
Range	**31 - 52 mm**		**39 - 88 mm**		**28 - 50 mm**		**52 - 83 mm**	

The ANOVA confirmed that strength of attachment differed significantly at the four sites ($n = 240$, $\alpha = 0.05$, $p < 0.001$). Bonferroni pairwise comparisons revealed that animals inhabiting the exposed low shore were more difficult to dislodge than animals residing in the high zones of both exposed and sheltered shores (experimentwise $\alpha = 0.05$, $p < 0.001$), but were no different to those of the sheltered low shore ($p > 0.1$). The sheltered high site, sheltered low site and exposed high site were all significantly different to one another in terms of attachment strength ($p < 0.001$). Another interesting result is that mussels within the bed, at all sites, were more firmly attached two weeks after the experimental clearance ($p < 0.001$). The interaction between site and time was non-significant ($p > 0.4$).

The shell lengths of mussels was dependent on the site in which they were found. Individuals at the exposed low site were similar in length to those at the sheltered low site (Table 4.2), and animals inhabiting these lower sites were larger than those at the higher elevations. Mussels in the sheltered high zone were smallest.

ANOVA showed that the differences in length between sites was statistically significant ($n = 240$, $\alpha = 0.05$, $p < 0.001$). The Bonferroni comparisons detected that the exposed low zone individuals were significantly larger than their counterparts in the exposed high and sheltered high zones ($p < 0.001$) and were equal in length to the sheltered low mussels ($p > 0.5$). The latter three sites were all statistically different to one another in terms of shell length ($p < 0.001$). Shell length did not vary temporally - lengths recorded at the time of experimental clearance were equivalent to lengths recorded two weeks later ($p > 0.8$) This result is noteworthy because it infers that differences in attachment strength between these two sampling periods were not attributable to differences in length.

2.2 Force-length relationship

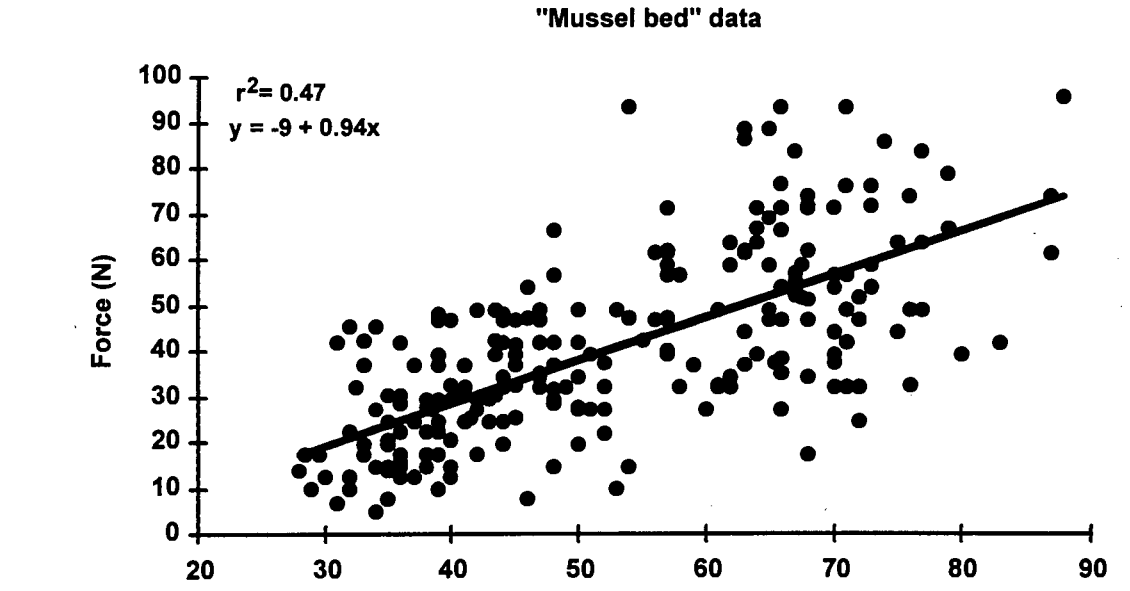
Linear regression analysis revealed a substantial correlation between shell length and strength of attachment, both for within-mussel bed individuals and for mussels situated on plot edges ($p < 0.005$). For "mussel bed" data, 47% of the variation in force is explained by length, whereas 37% of this variability is accounted for in "edge" animals (Figure 4.1). This brings to light that the length-force relationship varies under different conditions and cannot be extrapolated across them. Moreoever, the regression on "mussel bed" data points to the fact that an effect of shore height on attachment strength cannot be isolated from the discrepancy in sizes of animals and more specifically, that differences in strength of attachment between sites (section 2.1 above) are at least partly attributable to size differences.

2.3 Within-site comparisons

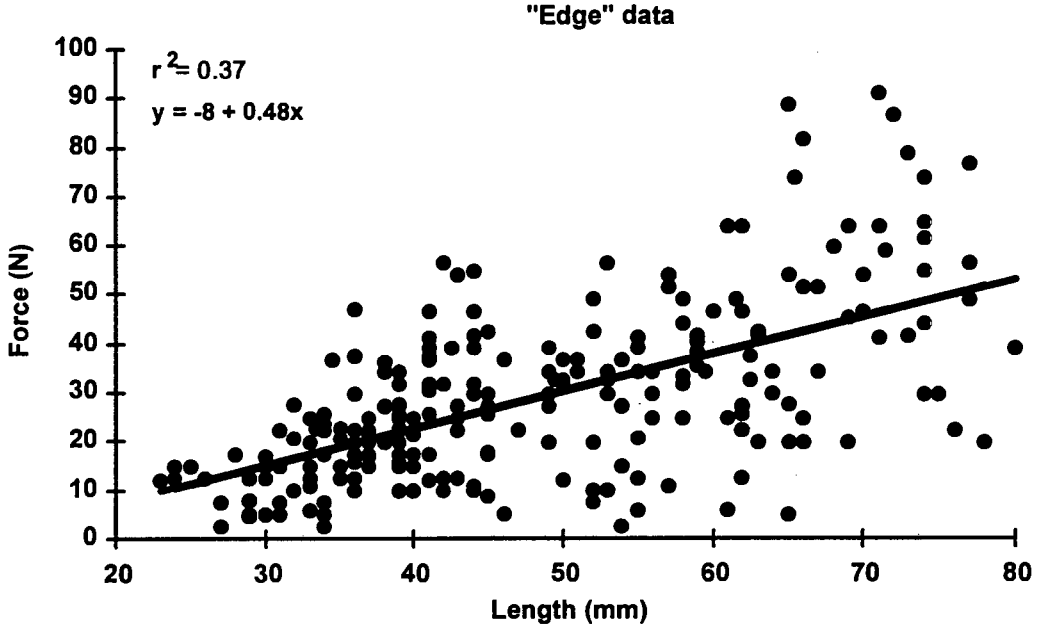
2.3.1 Edge effects

Figure 4.2 illustrates that mussels situated within the extant mussel bed were more difficult to dislodge than those situated on the edges of plots, at three of the four sites, at the time that the growth plots were cleared (time 1). There appears to be little or no difference in attachment strength between "mussel bed" individuals and "edge" individuals in the sheltered high site. It is noteworthy that the "edge" effect evident at the exposed low and high shore sites, as well as at the sheltered low site is less obvious two weeks after the initial clearance of growth plots.

For each ANCOVA (one per site), the regression slopes were tested for homogeneity and were always found to be parallel to one another ($\alpha = 0.05$, $p > 0.2$). There were significant differences between treatments for each analysis ($\alpha = 0.05$, $p < 0.001$). A Bonferroni post hoc comparisons test was subsequently run for each ANCOVA to determine which treatments were significantly different at the site being analyzed. The difference in attachment strength between "mussel bed" and "edge" animals, at time one, was statistically significant at the exposed low site ($n = 112$, $p < 0.005$), at the exposed high site ($n = 115$, $p < 0.05$) and at the sheltered low site ($n = 113$, $p < 0.005$). There were no differences in attachment strength in the sheltered high zone ($n = 113$, $p > 0.6$). At time two, attachment strength of "mussel bed" animals was statistically equivalent to that of mussels situated on plot borders at the exposed low site ($p > 0.6$), at the exposed high site ($p > 0.3$) and at the sheltered high site ($p > 0.99$). In the sheltered low zone, however, mussels within the bed were still more firmly attached than mussels situated on the edge of the bed ($p < 0.001$).

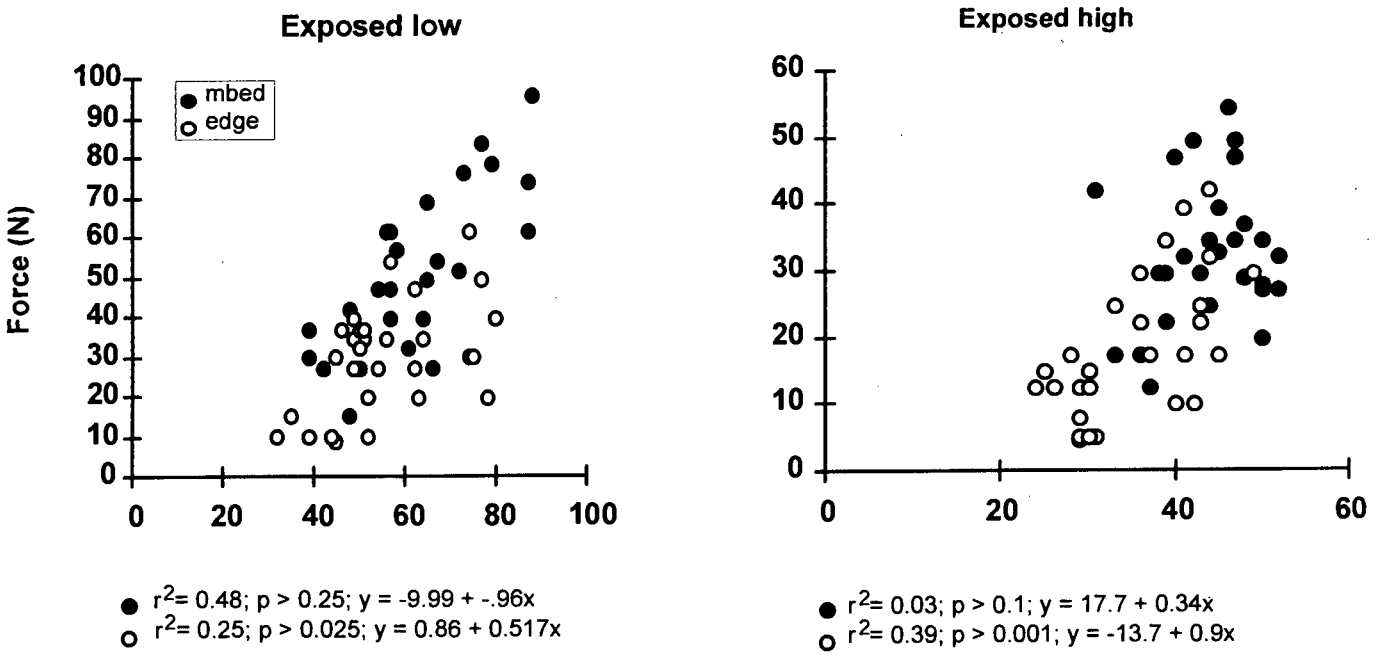


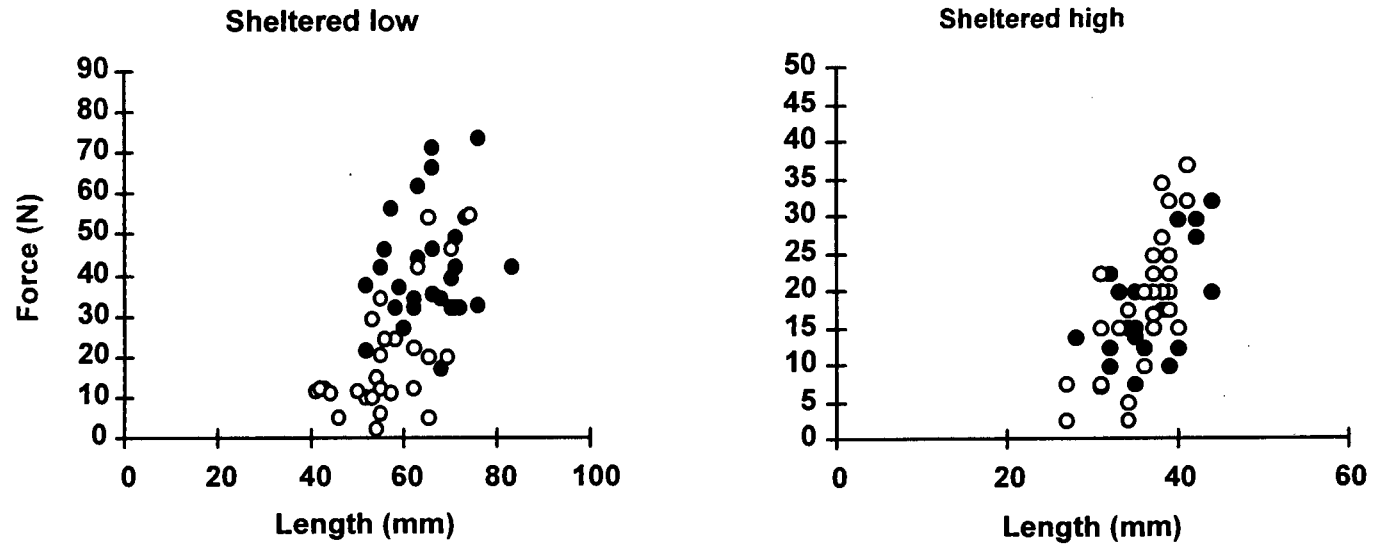
a)



b)

Figure 4.1 Linear regression of force (N) on length (mm) for a) mussels situated with the mussel bed and b) mussels situated on the edge of cleared plots. Data from sheltered and exposed, high and low shores are recorded; n = 240, $p < 0.005$ for each plot.



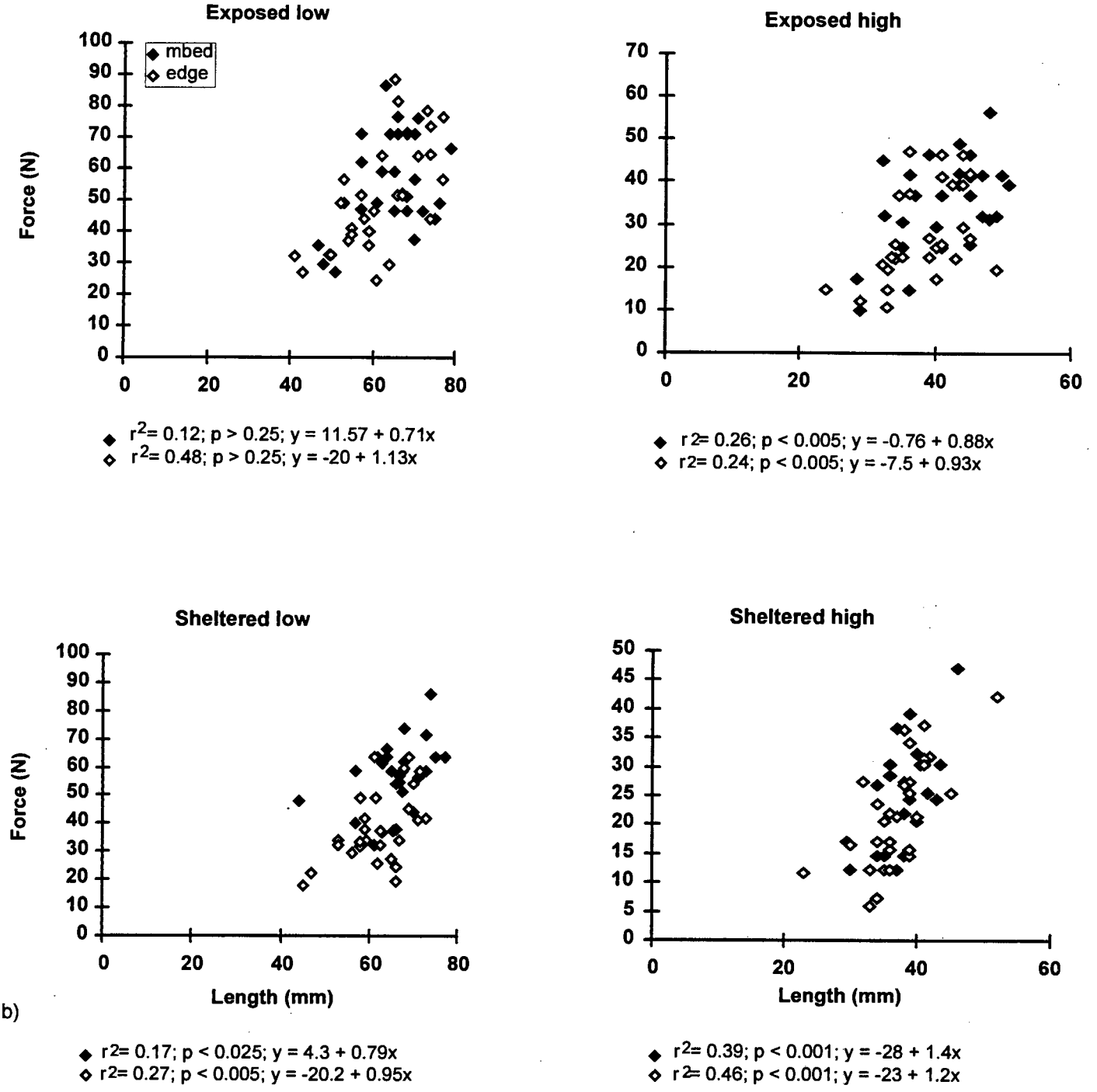


a)

● r2= 0.03; p > 0.1; y = 21.6 + 0.31x
○ r2= 0.38; p < 0.001; y = -40.2 + 1.07x

● r2= 0.57; p < 0.001; y = -19 + 0.99x
○ r2= 0.57; p < 0.001; y = -40.6 + 1.7x

Figure 4.2 continued on following page



b)

Figure 4.2 Force-length plots for sheltered and exposed, high and low shores for a) time 1 and b) two weeks later. Data are collected from within the mussel bed (mbed) and from the edges of cleared plots (edge). Correlation coefficients and p-values are given for each regression, as are the regression equations. Time 1 and time 2 plots are separated for easier reference, but ANCOVA was performed on both initial and final measurements (for each site).

2.3.2 Temporal variation

Mussels positioned on the edges of plots had elevated attachment strengths two weeks after the experimental clearance of these plots. On average, mussels in the exposed low zone raised their strength of attachment by 21 Newtons (Table 4.3). Attachment strength increased by 19 Newtons in the sheltered low zone, was raised by 12 Newtons in the exposed high zone and by only 3 Newtons in the sheltered high zone. On the whole, these mussels increased their attachment strength by approximately 1.8 times more than their counterparts within the bed, over the same period (cf. Table 4.2).

Table 4.3 Average attachment strength (+S.D.), in Newtons, of animals collected from the edges of cleared plots in exposed, high and low shores and sheltered, high and low shores. Measurements taken at the time of clearance are given with those recorded two weeks later.

Exposed zone				Sheltered zone			
High shore		Low shore		High shore		Low shore	
Initial	Final	Initial	Final	Initial	Final	Initial	Final
18 (10)	30 (13)	30 (14)	51 (19)	19 (9)	22 (9)	21 (15)	40 (18)
n = 30	n = 30	n = 30	n = 30	n = 30	n = 30	n = 30	n = 30

The Bonferroni multiple comparisons test (performed subsequent to ANCOVA, see section 2.3.1 above) concluded that there was a significant temporal effect in attachment strength of "edge" mussels, for both exposed sites and for the sheltered low-shore site. Attachment of these animals was significantly stronger two weeks after the start of the experiment; $p < 0.001$ for the exposed low and sheltered low sites, $p < 0.05$ for the exposed high-shore analysis. This suggests that mussels at these sites did respond to their increased vulnerability to wave action by producing more byssal threads. At two of the three sites "edge" individuals were as firmly attached as "mussel beds" just two weeks after the experimental plots were cleared (section 2.3.1). This is despite the fact that animals within the mussel bed were more firmly attached at this time than at the previous spring tide (see section 2.1 above). There was no (statistical) temporal variation in strength of attachment of the "edge" mussels in the sheltered high zone ($p > 0.99$).

DISCUSSION

The phenomenon of "uprooting" of areas of mussel bed by storm-induced wave action is a common occurrence (see Paine and Levin, 1981; Sousa, 1985; Witman, 1987), but has not yet been formally described in South Africa where winter storms commonly dislodge areas of mussel bed, particularly on the wave-exposed west coast (Branch, pers. comm.). At the Camps Bay study site in 1993, a 1.4 m^2 area of mussel bed was dislodged from the low zone

on an exposed rock after severe storms beset the west coast. The area affected at this particular site was significantly greater than at both high and low-shore sheltered sites as well as the exposed, high shore. More quantitative measurements at fixed experimental quadrats (Table 4.1) confirm this pattern. It is important to quantify the size of patches and their location for two reasons: firstly, they may be used to create working models of landscape disturbance that predict system dynamics over different spatial and temporal scales, and secondly, such models could be used to reconstruct past disturbance events (see, for example Paine and Levin, 1981). With this information one could, for example, characterize areas of coastline in terms of a disturbance gradient.

Strength of byssal attachment for mussels in the Camps Bay area varied with respect to their location on the shore. Specifically, *M. galloprovincialis* exposed to heavy wave action in both the exposed and sheltered low-shore sites required more force to be displaced than those in the upper intertidal sites, where wave action is not as great. This was not unexpected since individuals exposed to greater hydrodynamic pressures presumably need to be more firmly attached to ensure their persistence in this environment. The results accord with previous studies on *Mytilus edulis*. Price (1980, 1982) found that *M. edulis* exhibits seasonal variation in byssal attachment strength, apparently in response to changing environmental conditions. It increased byssal strength when exposed to strong wave action during winter months, but after experiencing about one month of weak winds, strength declined. It is likely that in the absence of extreme wave action no new threads were produced and older threads had begun to degenerate. While the former procedure can be controlled by mussels, the process or rate of degeneration cannot, since decay of byssus threads is probably due to the presence of fungi associated with them (see Vitellaro-Zuccarello, 1973).

It is worth recounting that shell length accounted for 47 percent of the variation in strength of attachment for individuals situated within the mussel bed. This association is of critical importance when interpreting the relationship between byssal attachment and shore height because of the relative sizes of mussels in these areas - mussels situated at the lower tidal elevation in both sheltered and exposed areas were larger than the mussels situated in the higher zones. While some of the discrepancy in attachment strength may be attributable to the relative lack of environmental stress (e.g. desiccation and temperature) in the lower intertidal zone, for the most part it appears that the larger size of animals in the low-shore sites determines the divergence. The fact that mussels in the high zones seemed relatively unaffected by the storm regardless of their relatively weak attachment strength points to the suggestion that animals lower down on the exposed shore experienced sudden, significant changes in environmental conditions. It is noteworthy that the section of low exposed shore experienced relatively strong, turbulent wave action and it is likely that this, in combination with

sheer force resulted in the demise of these mussels. To add to this, animals in this area would have been more susceptible to disturbing hydrological forces such as drag and accelerational forces by virtue of their greater size (see Sousa, 1985). Animals residing in the low zone of the sheltered area were relatively unaffected by the storms, despite their attachment strength being similar to that of mussels in the exposed low zone. These findings (and personal observation) suggest that hydrological strains at the sheltered (low) site are insignificant by comparison to the exposed low zone. The results certainly indicate the need for measuring all aspects of the environmental variable/s thought to determine observed patterns. With such measurements at hand, the predictiveness of models of disturbance-determined community dynamics will be dramatically enhanced.

Another significant finding of the current investigation was that mussels situated on the edges of manually cleared plots were easier to detach than individuals found within the mussel bed, with the exception of mussels at the sheltered high-shore site. The "edge" effect may be attributed to the accidental destruction of byssus threads when the plots were cleared and/or to their not being wedged between neighbouring individuals. Just two weeks after the experimental clearance of mussel bed, individuals on the fringe of plots became significantly more difficult to remove than similarly positioned animals at the start of the experiment (again, with the exception of the sheltered high-shore site). This points to the ability of mussels to respond to an environmental pressure (in this case, wave-exposure). Another finding that supports this conclusion is that mussels on the edge enhanced their attachment strength by 1.8 times that of animals within the bed during the same period. It is not known what induced the within-bed mussels to increase their attachment strength nor whether, given sufficient time and/or suitable conditions, the animals on the edges of beds in the sheltered low site would become as securely adhered to the substrate as they did at the exposed low and the exposed high sites. The potential effect of length in these comparisons was eliminated by employing site-by-site (covariate) analyses.

The results do suggest an explanation for why the storm damage was evident only around previously cleared quadrats, since weakened attachment would have left those mussels vulnerable to strong wave action. *Time 1 and time 2 data do not differ because of body size differences*). The mussels presumably require an appropriate interval from the pressure of wave action to allow for compensation in attachment strength. Unfortunately, no data could be gathered to make these conclusions unequivocal because most of the mussel bed in the exposed low shore was subsequently removed, so that there remained little or no *undisturbed* portion of mussel bed to act as a control.

There is some debate as to whether the exposed edges of clearings in mussel beds are more vulnerable to disruption than intact areas of mussel bed (Sousa, 1985). The coalescence of smaller neighboring patches into a single large patch may lead one to conclude that patches effectively grow in size by erosion along their edges. This conclusion may, however, be unfounded, particularly when observations are infrequent (see Sousa, 1985). Paine and Levin (1981) provide a model for patch formation and death for *Mytilus californianus* on the exposed rocky coast of Washington. The size of patches at birth was highly variable and the mechanisms by which these patches were created are not understood. There is no mention of erosion of mussel beds along their patch edges and their assumption is that the size of new patches at their first observation is their birth size. While the disregard of edge erosion *per se* should not affect the outcome of their model, it is precisely this factor that might be a mechanism acting on the formation and growth of patches. The mechanisms that exist are likely to be complex and unique to particular areas of coastline but identifying and quantifying them would enhance the predictiveness of models of this nature. The consequences of edge effects have been reported extensively in the literature, principally in terrestrial systems (e.g. Yahner, 1988; Laurance, 1991; Rolstad, 1991) and the edge effects demonstrated here for in mussel beds cannot be ignored.

Patches do occur naturally at the Camps Bay study area - during previous and subsequent visits to Camps Bay, large bare patches were seen on the same exposed rock on which these experiments were performed. Similar observations of storm-induced damage have been recorded elsewhere; Asmus (1987) reported the removal of *M. edulis* beds by winter storms, leaving only bare sand flats. Nehls and Thiel (1993) noted that the number of *M. edulis* beds in the Wadden Sea declined after major storms. In the Gulf of Maine on the east coast of the United States storm disturbance created patches in subtidal *M. modiolus* mussel beds (Witman, 1987). The formation of wave-induced patches in *Mytilus californianus* beds was shown to vary seasonally along the Pacific coast of North America (Paine and Levin, 1981). Once disruption of *M. californianus* beds by storms has begun, the mussel bed is quickly washed away.

Several studies have investigated byssus thread formation under different environmental conditions. Maheo (1970, in Smeathers and Vincent, 1979) found that *M. edulis* increases the number of threads when exposed to increased turbidity. Allen *et al.* (1976) found that the number of threads produced by *M. edulis* varied with salinity - the number of threads increased with salinity but the response was also dependent on the size of the animal. Van Winkle (1970) reported the inhibition of thread production of *Modiolus demissus* by red tides. Another interesting finding of the study was that animals that had been exposed to air for long periods showed an enhanced rate of thread formation. This is of particular interest since high-

shore *M. galloprovincialis* may exhibit similar capabilities, which could benefit them under certain conditions. One should however, be wary of extrapolating since different species do not necessarily respond to environmental stresses in the same fashion - for example, the rate of thread formation in *M. edulis* was reduced in high water temperatures, but was unaffected in *M. demissus* (Van Winkle, 1970). While the rate of thread production (and numbers produced) is obviously relevant, a critical issue is that the mechanical properties of mussel byssus threads can change under certain conditions - such as whether they are wet or dry (Smeathers and Vincent, 1979). In other words, the advantage afforded by increased rates of byssus formation might be offset by mechanical constraints.

An additional environmental factor which needs to be explored with respect to the strength of byssal attachment is the type of substrate on which they are found. While byssus threads are a suitable substrate for the settlement of young mussels (Seed, 1969) larger mussels that are attached to this substrate can be detached with relative ease. At Camps Bay, animals that are attached to byssus threads are less secure than those directly attached to bare rock or barnacles (personal observation). Mussels that were inundated with sand, for example in some areas of the sheltered zone in Camps Bay, were also generally easy to remove. Although these confounding factors were avoided when the measurements of attachment strength were made, they may additionally affect the way in which the population responds to wave action. A final suggestion is to sample the entire range of mussel sizes where possible to completely eliminate the confounding effect that length has on strength of attachment. This was not achieved in the current study for two reasons: firstly, mussel beds in the exposed low zone are multilayered and smaller mussels tend to attach themselves to larger adults rather than to the underlying rock. The result is that these mussels are less firmly attached than if they were directly attached to rock. Secondly, mussels in the higher intertidal zones do not achieve the same size as those inhabiting lower zones, with the result that values out of this range need to be extrapolated, which may lead to misleading conclusions (see e.g. Zar, 1984).

In conclusion, strength of attachment was demonstrated to be higher in low-shore mussels than in high-shore mussels at both exposed and sheltered sites, one of the main reasons being their larger size. Despite their tenacity, these low-shore, exposed-site mussels suffered greater losses during storms, inferring greater hydrodynamic stresses low on the shore. The relatively weak attachment of mussels on the edge of patches may have contributed to these losses, particularly if storms struck too frequently for compensatory strengthening of attachment to have occurred.

GENERAL DISCUSSION AND CONCLUSIONS

A number of interesting population patterns occurred in this study of *Mytilus galloprovincialis* at Camps Bay and Groenrivier, on South Africa's west coast. There was extreme spatial variability in patterns of mussel cover, total mussel densities and densities of recruits as well as size structure, which was, for the most part, related to wave exposure and tidal elevation. Mussel cover, total densities and recruitment increased with increasing wave exposure. While mussel cover tended to decrease upshore, the reverse was true for mussel densities. The latter finding is most unusual, in view of the physiological stresses usually exerted on intertidal organisms inhabiting upper shore levels, as a consequence of high insolation and decreased water inundation (e.g. Lewis, 1964; Stephenson and Stephenson, 1972; Connell, 1972, 1975). By the same argument, one would expect recruit densities to decrease upshore, but the opposite was found, and no temporal variability existed in this pattern. The fact that *M. galloprovincialis* is relatively tolerant of heat stress and dessication (Griffiths *et al.*, 1992; Hockey and van Erkom Schurink, 1992) offers an explanation for these unexpected results.

The maximum size attained by animals inhabiting wave-exposed areas was greater than that of mussels located in more sheltered areas, and mussels at the upper levels of the intertidal zone tended to be smaller in size than those in lower zones. The size structure of mussels at Camps Bay may be explained by the differential growth rates of animals at different sites, as determined by following the growth of labelled mussels and by cohort analysis. While growth was not investigated at Groenrivier, it is almost certain that these patterns are attributable to differences in growth rates. Future studies need to quantify food availability and nutrient uptake under different conditions, at the same time that maximum sizes achieved and growth rates are recorded to establish the exact relationship between these factors. Additionally, the potentially confounding factor of packing density on growth rates and/or shell shape should be examined.

Mortality rates of young mussels (as depicted in Figure 3.2, from cohort analysis) at different sites in Camps Bay seem to reflect the degree of wave exposure experienced by mussels in these areas. Survival was exceptionally low in the exposed low zone, was relatively low at the exposed low-shore site and at the sheltered low-shore site. Mortality was very low at the sheltered high site. Similar results were obtained for "tagged" adults, except that an unexpectedly large number of mussels was lost from the sheltered high-shore site. This may have been due to human interference and is unlikely to reflect wave-induced losses. A separate analysis of newly settled mussels revealed that, over a two month period, mortality rates in the sheltered low zone were similar to those in the exposed low zone. Long-term monitoring of a similar nature would determine whether differences in post-settlement mortality

emerge after longer periods and whether temporal variation in mortality rates occurs. The causes of temporal variability need to be examined, if they exist.

The importance of recruitment in regulating community structure is a "hot" topic in ecology (e.g. Gaines and Roughgarden, 1985; Menge and Farrell, 1989; Petraitis, 1990, 1991) but its relationship to final adult densities is not well understood (e.g. Fairweather, 1991). Results indicate that, on the whole, very little of the variability in adult densities is accounted for by recruit densities at Camps Bay. There was a great deal of spatial and temporal variation in this relationship, as well as in the significance of the relationship. Recruit densities and total densities seem to be highly correlated at both Camps Bay and Groenrivier, especially on wave-swept shores where recruitment is particularly high.

Similarities in population demography between the semi-exposed region of Groenrivier and the sheltered area at Camps Bay, determined by cluster analysis and multidimensional scaling, probably reflect similarities (historical or immediate) in environmental parameters at these locations (Clarke and Warwick, 1994). The same may be said for similarities in population structure between the two low-shore sites and the two high-shore sites at Camps Bay. These and other findings would be corroborated by measuring the environmental parameters that are relevant to the animals being studied. Such measurements would allow one to predict the population/community patterns that occur within a given range of environmental conditions, and having established these relationships, one could potentially characterize regions in terms of environmental conditions when only the population structure has been recorded.

The effect of winter storms on mussel beds are often dramatic (e.g. Nehls and Thiel, 1993) and this study has shown the spatial dependency of its influences. Moreover, the fact that bare patches were always adjacent to manually cleared plots is correlated with "edge" effects - mussels situated within the mussel bed were more firmly attached than mussels on plot edges. "Edge" mussels were able to compensate for their increased vulnerability to wave action by becoming more firmly attached after two weeks and were generally as firmly attached as their within-bed counterparts at this time.

The relative contribution of biotic and abiotic processes on mussel population structure were beyond the scope of this study. Indications are that is is the interplay of recruitment patterns, biological processes and physical factors that determine the population structure of *M. galloprovincialis*. It is likely that the relative importance of these factors is dependent on wave exposure and tidal elevation - for example, biological interactions may be more important in structuring communities in sheltered areas while physical factors may determine most of the

variability in populations on wave-swept shores. The key to understanding the dynamics of these mussel populations lies in further research.

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APPENDIX 1:

Tables 1 and 2: Strength of attachment and shell length of mussels recorded concurrently in exposed, high and low shores and sheltered, high and low shores. Data are collected from mussels residing within the extant mussel bed and on the edges of the mussel bed at the time of plot clearance and two weeks thereafter (Chapter four).

Table 1: Force (in Newtons) and length (mm) data for animals collected from within mussel beds at the time of experimental clearance (time 1) and two weeks later (time 2). Data are recorded for both exposed and sheltered zones. Numbers in bold in the last row are the averages of each column.

Time 1								Time 2							
Exposed zone				Sheltered zone				Exposed zone				Sheltered zone			
Low shore		High shore		Low shore		High shore		Low shore		High shore		Low shore		High shore	
Force	Length	Force	Length	Force	Length	Force	Length	Force	Length	Force	Length	Force	Length	Force	Length
69	65	17	36	47	66	32	44	71	66	32	47	64	62	17	30
47	57	12	37	42	71	25	39	71	57	42	47	54	70	30	44
7	46	42	31	47	56	29	42	49	61	49	44	32	61	28	36
93	54	32	41	42	55	27	42	47	65	17	29	52	68	30	41
15	48	37	48	34	68	17	39	77	66	37	45	64	75	27	39
61	57	32	45	17	68	10	39	29	48	47	39	67	64	22	38
29	39	29	39	62	63	15	40	47	68	10	29	59	73	25	43
61	56	27	50	56	57	49	50	37	70	30	35	37	63	47	46
27	50	39	45	32	58	20	44	59	65	42	36	64	64	26	42
39	57	20	50	37	59	22	32	49	53	41	45	48	44	17	42
54	67	25	44	37	52	12	32	88	65	47	45	37	66	22	36
37	39	54	46	22	52	15	34	62	57	32	33	61	63	27	34
83	77	22	39	34	62	5	34	71	68	45	32	59	65	12	37
47	54	49	42	27	60	15	35	47	57	15	36	40	57	15	35
56	58	49	47	32	71	20	33	51	68	56	48	10	53	21	40
42	48	29	38	42	71	12	32	86	63	37	41	44	70	42	33
88	63	34	44	44	63	15	35	93	66	47	44	57	67	37	33
32	61	29	43	49	71	12	36	59	62	37	37	56	71	45	34
27	42	28	48	66	66	14	35	56	70	26	45	59	57	27	38
39	64	47	40	32	62	25	37	35	47	42	44	59	68	15	38
49	77	47	47	83	67	7	35	71	70	29	40	55	67	12	30
74	87	34	44	42	83	12	40	76	71	31	48	25	72	30	36
49	65	17	33	32	72	10	32	47	72	32	49	86	74	15	34
27	66	27	50	54	73	15	35	72	68	25	35	38	66	21	35
52	72	42	44	71	66	29	40	71	64	15	54	64	77	32	40
61	87	34	47	74	76	17	38	67	79	42	50	93	71	16	36
96	88	29	43	35	66	14	28	44	75	39	51	72	73	25	39
78	79	27	52	32	70	20	35	52	67	39	44	74	68	39	39
76	73	34	50	39	70	15	40	49	76	25	41	54	66	48	39
39	80	32	52	32	76	7	31	27	51	66	48	62	68	37	37
52	**63**	**33**	**44**	**43**	**66**	**18**	**37**	**59**	**65**	**36**	**42**	**55**	**66**	**27**	**37**

Table 2: Force (in Newtons) and length (mm) data for animals collected from the edges of plots at the time of experimental clearance (time 1) and two weeks later (time 2). Data are recorded for both exposed and sheltered zones. Numbers in bold in the last row are the averages of each column.

Time 1								Time 2							
Exposed zone				Sheltered zone				Exposed zone				Sheltered zone			
Low shore		High shore		Low shore		High shore		Low shore		High shore		Low shore		High shore	
Force	Length	Force	Length	Force	Length	Force	Length	Force	Length	Force	Length	Force	Length	Force	Length
39	49	10	40	5	46	15	40	49	52	21	32	49	58	37	41
15	35	22	43	10	52	17	37	32	50	25	40	37	63	27	39
34	51	29	36	34	55	32	41	27	43	55	44	27	65	32	42
34	49	5	31	12	43	32	39	32	41	41	41	49	62	12	33
10	52	4	29	25	58	22	39	52	57	29	44	34	53	12	35
9	45	17	41	12	41	25	37	40	59	39	43	32	58	42	52
34	56	7	52	29	53	34	38	37	54	22	34	86	72	22	37
10	39	8	29	12	55	17	39	56	53	37	36	59	72	17	30
32	50	39	41	12	42	10	36	41	55	26	34	74	66	34	39
54	43	34	39	21	55	15	37	35	59	56	42	22	47	15	39
10	44	22	43	20	69	25	39	91	71	11	33	25	66	16	39
10	32	15	25	42	63	15	31	64	71	15	33	20	66	6	33
29	45	5	29	47	70	7	27	47	60	47	41	32	53	17	34
54	57	15	30	2	54	22	31	25	61	47	36	18	45	22	40
37	50	12	29	15	54	17	34	32	50	12	29	29	56	12	36
34	64	12	26	11	44	20	39	44	58	20	33	32	63	12	42
27	54	17	28	12	50	20	38	88	65	39	44	45	69	24	34
37	46	12	24	5	65	37	41	77	77	23	35	38	59	16	36
27	49	25	43	12	55	25	39	81	66	15	24	34	60	26	39
20	52	22	36	6	55	7	27	65	74	27	45	6	61	12	23
49	77	17	45	22	62	7	31	22	76	27	39	34	67	31	41
61	74	29	49	22	62	25	37	74	74	17	40	60	68	21	35
20	63	22	36	12	62	5	34	52	66	23	39	26	62	36	38
37	51	17	37	54	65	27	38	64	62	20	49	42	73	7	34
39	80	32	44	42	63	15	33	52	67	23	34	41	71	22	36
29	74	10	42	55	74	20	37	78	73	22	43	54	70	17	36
29	75	12	30	11	57	2	34	39	55	37	35	64	61	30	41
27	62	25	33	25	56	20	36	29	64	47	44	64	69	27	38
20	78	5	30	10	53	22	37	44	74	26	41	33	58	26	45
47	62	42	44	20	65	2	27	56	77	42	45	42	59	27	32
30	**55**	**18**	**36**	**21**	**57**	**19**	**36**	**51**	**62**	**30**	**38**	**40**	**62**	**22**	**37**